

SALIX HERBACEA AND THE ALPINE
SNOW-BED ENVIRONMENT

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***SALIX HERBACEA* AND THE ALPINE SNOW-BED ENVIRONMENT**

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S. Wijk

CONTENTS

Förord

Introduction and summary of results 7

- I. Alpine gradients of snow cover and the distribution of vascular plant species. 11
- II. Performance of *Salix herbacea* in an alpine snow-bed gradient. - Journal of Ecology, 74. (1986). In press. 29
- III. Influence of climate and age on annual shoot increment in *Salix herbacea* . - Journal of Ecology, 74. (1986). In press. 39
- IV. Age structure of *Salix herbacea* shoots in an alpine snow-bed. 47

Alttryck ur Teknisk Tidskrift 1905.

Den naturvetenskapliga stationen vid Vassijaure i Torne lappmark.*

De som nu på Ofotenbanan helt bekvämt förflytta sig till Torneträsk, kunna näppeligen riktigt uppskatta de svårigheter, med hvilka naturforskare och ingenjörer förut hade att kämpa under arbetena i dessa trakter. Att stundom natt efter natt nödgas krypa in i sin sofsäck med genomvåta kläder eller att för köld få nöja sig med en eller ett par timmars dålig sömn flera dygn på rad, ej sällan med endast ett klippblock som skydd mot den isande fjällvinden — sådant fick räknas som bagateller. Man måste bemöda sig att bannlysa hvarje veklig tanke på människoboningar, säng, lagad mat o. d., emedan sådana tankar kunde blifva frön till feg själfuppgifvelse och reträtt. Tärande kändes ofta omöjligheten att under månader erhålla underrättelser från den yttre världen. Vanligen var handtlangare- och bärareproblemet ytterst svårlost. Det var oerhördt dyrt redan att komma ditupp vare sig från svenska eller norska sidan. Endast för en hastig tur från Jukkasjärvi, där skjutsskyldigheten upphörde, nödgades man på 1880-talet vanligen beräkna 45 å 50 kr. pr roddare. Skulle man sedan ha folk för arbetena eller fortsatta vandringar, funnos ju under som-

* Följande uppsats är det väsentliga innehållet af ett föredrag vid Stockholms Naturvetensk. Förenings »tredjedelssekelsfests» den 25 sisl. Februari.

F Ö R O R D

Den 28 Juni 1977 klev jag på Lapplandspilen med destination Abisko Östra. En försmak av Abiskos fjällvärld hade jag fått redan året innan, då jag som snyltgäst hos Urban och Birgitta också hade tillfälle att se "Vetenskapen" från insidan. Men nu gällde det allvar. I bagaget hade jag förutom fältutrustning, frystorkat och djungelolja, också några tankar och idéer om gradientanalyser och växters utbredningsgränser, allt noga formulerat i en s.k. forskningsplan. Mats Sonesson hade därtill försett mig med en skrift om snölegor av Gjaerevoll, vilket gjorde det hela lite mera konkret. Så stod jag så småningom vid kanten av en snödriva omgiven av Vassijaures blöta dis och försökte hitta några gemensamma nämnare mellan teori och verklighet. Sedan dess har det blivit många fältarbetsresor till det eviga duggregnet. Konfrontationerna mellan idé och verklighet har lett till ständiga omprövningar, förkastande och nytillskott av hypoteser och nu, just som jag börjar ana var svaren på mina frågeställningar står att finna, är betänketiden ute och det är dags att presentera resultatet.

Under den tid arbetet pågått har det hänt ett och annat inom västekologin, populationsekologin har definitivt slagit rot också bland botanister och nygamla tankar om växtdelar som individer i en subpopulation har dammats av. Detta har inte kunnat undgå att färga mitt arbete och är en orsak till att tre av de fyra artiklarna handlar om skotten hos dvärgvide och endast en knyter an till de ursprungliga idéerna om växtarternas utbredningsmönster. Men förskjutningen i arbetets inriktning är också en följd av att varje undersökning leder till nya frågor snarare än till definitiva svar. Min forskning har också inspirerats och påverkats av många forskare från olika håll i världen som jag kommit i kontakt med i Abisko. Jag vill här ta tillfället i akt att rikta ett stort tack till Terry Callaghan och Jeremy Flower-Ellis som alltid varit öppna för diskussioner och välvilligt ställt upp med synpunkter och kritik på "Salix-manuskripten" i ett oräkneligt antal versioner; Sven Jonasson och David Goodall som gjort tappra försök att nysta upp och kritisera mina egensinniga metoder för gradientanalys. Tack också till David Tilles som har gjort den engelska texten förståelig även för icke svensktalande.

Fältarbetet har utförts med Abisko Naturvetenskapliga Station som ovärderlig bas och reträttort. Mats Sonesson, stationens föreståndare, tillika min handledare, har från första början gett mig fria händer och nyttiga resurser och har aldrig (för mig) visat några tvivel på min verksamhet, vilket är något av det bästa stöd man kan få. Personalen bidrar i högsta grad till den positiva atmosfär som råder på ANS och finns alltid till hands när man bäst behöver dem. Särskilt tack till Nils-Åke, Frid, Anders, Linnea, Bengt och Sune. I fält har jag dessutom haft stor hjälp av Bo Björnsäter och Leif Unosson.

Under de många fältsäsongerna har Abiskostationen varit en arbetsplats och ett hem som jag delat med många människor. Där har jag alltid kunnat få respons på nya huqskott och många goda råd om allt ifrån pyranometrar till brödrecept. Tack för en fin och stimulerande gemenskap - Staffan, Olle, Urban, Birgitta, Björnur, Bjartmar, Jöran, Strömquist, Brita, Bengt och alla mer eller mindre tillfälliga medlemmar i "StarTeam".

Arbetskamraterna vid Växtekologiska institutionen måste jag tacka kollektivt då så många bidragit med strån till stacken. Om någon ska nämnas är det Claes, min ständige bordsgranne och vän som aldrig låter ett utrop hänga obesvarat kvar i luften.

Slutligen vill jag tacka mina närmaste, Elisabet som, förutom att ha stått vid spisen och fött barn, gjort ett större del av detta arbete än någon annan (möjligen undantaget mig själv), i fält, på lab, repro, korrektur m.m., m.m.

Annika ☀

Mina föräldrar, utan vilka detta arbete aldrig hade blivit utfört.

Lund den 19:e mars 1986.

INTRODUCTION AND SUMMARY OF RESULTS

Alpine habitats are greatly influenced by microclimatic conditions which are closely associated with the topography. Fell-fields on ridges may remain bare of snow throughout the winter, and are exposed to low temperatures and wind abrasion. In the depressions, several meters of snow accumulate which does not melt completely until late summer. These habitat extremes may occur within a short distance of each other, and leeward slopes often show steep environmental gradients.

Previous studies of the vegetation along snow cover gradients in Scandinavia have been mainly concerned with the distribution of plant communities; they generally included very few details on environmental conditions. Despite the lack of data, it has been generally accepted that the distribution and duration of snow cover is the primary factor controlling the distribution of plant species along these gradients.

Indeed, many factors that vary along the gradient are related to the snow conditions, e.g. growing season length, winter temperatures, mechanical snow pressure, soil moisture during snowmelt, and grazing intensity. However, these gradients are complex, and other factors are more directly associated with topography, e.g. microclimate and soil moisture during the growing season. Several factors are also influenced by the plant cover itself as, for instance, soil profile, nutrient availability, and competition.

The aim of the work presented in paper I was to interpret the distribution pattern of vascular plant species in snow cover gradients with respect to curve form and continuity, and also to determine the importance of snow duration. The vegetation was mapped in eleven transects, and the snowmelt was recorded for three successive years. There appeared to be no simple relationship between species distributions and snow duration, but the general distribution pattern was very similar in all transects. Therefore the species distribution curves were also calculated for a gradient axis based solely on vegetational composition obtained from a weighted average ordination.

The majority of species showed individualistic distributions and there were no distinct community boundaries. However, there were sharp boundaries between the two species *Vaccinium myrtillus* and *Salix herbacea*. In transects where *V. myrtillus* was lacking, *S. herbacea* occurred on sites with melting dates earlier than were found in other transects. This suggests that the distribution of *S. herbacea* might be restricted to areas of later snowmelt by competition from *V. myrtillus*.

This hypothesis initiated a study of the changes in performance of *S. herbacea* along a snow cover gradient (paper II). Percentage cover, total biomass, and shoot density increased with increasing snow depth. However, the growth of individual shoots increased with decreasing snow cover and was greatest at the species' upper distribution limit, coinciding with the lower distribution limit of *V. myrtillus*. Maximum population density and maximum individual growth occurred at separate locations, supporting the competition hypothesis.

The changes in shoot growth along the gradient were disproportionately great as compared with the relatively slight differences in growing season length. A 20% increase in growing season length was associated with a three-fold increase in annual shoot increment. This suggests that the differences in shoot growth are also influenced by factors other than snow duration. Competition and grazing probably select young and vigorous plants at the upper end of the transect, while the life-spans of individuals, rhizomes, and shoots increase (and consequently productivity decreases) as the severity of the physical environment increases.

The climatic influence on shoot growth was the subject for paper III. A multiple regression analysis was made on shoot incremental growth with mean temperatures and precipitation for May - September, and shoot age as independent variables. The climatic variables contributed only slightly to the total variation in shoot growth, but about 80% of the between-year variation was accounted for by May and June temperatures of the year preceding growth. This was likely due to the influence of early summer temperatures on the rate of snowmelt and growing season length, which probably affected the accumulation of resources needed for the following year's shoot growth.

Growing season length probably also affects the number of shoots produced each year, since there was a positive correlation between June temperatures and the size of shoot age classes 1-6 years (paper IV).

The regression analyses also showed that shoot growth is highly age-dependent (paper III). Shoot incremental growth showed a logarithmic decrease with increasing shoot age. Since this decrease was already present the year after the shoot was formed, it was probably due to an internal redistribution of assimilates within the plant.

Averages and maximas of shoot age were considerably lower near *S. herbacea*'s upper distribution limit bordering *V. myrtillus* than elsewhere (paper IV). This could have been an additional effect of competition, but a higher level of grazing intensity might also have been important. Considerable losses of leaf area due to grazing by leaf beetles were observed particularly in the part of the gradient with an early snowmelt (paper II).

The age structure of the shoot population also varied along the gradient. By assuming that these age distributions are stable with time they can be interpreted as survivorship curves. The major part of the shoot population (associated with late snow release) showed low mortality during the first 6 years of growth, and thereafter the mortality remained at ca. 20%. Shoot survival was also initially high in the population that was associated with early snow release, but the mortality rate increased with age and there were no shoots older than 10 years.

The results presented here suggest clearly that conclusions about the factors controlling species distributions and plant growth which are based only on simple correlations with environmental data may be inaccurate. A species' response to its environment can be very complex, especially in clonal plants, since growth, reproduction, and mortality of plant parts are partly controlled by internal relationships (Fig. 1). Analyses of the changing performance of species along environmental gradients have here been shown to be a useful approach for elucidating some of the interrelationships involved. However, the hypotheses generated should also be verified experimentally. Such experiments have been started which will help us to better understand the ecology of *S. herbacea*. Hopefully, they will also reveal more of the fascinating secrets hidden along the alpine snow-bed gradients.

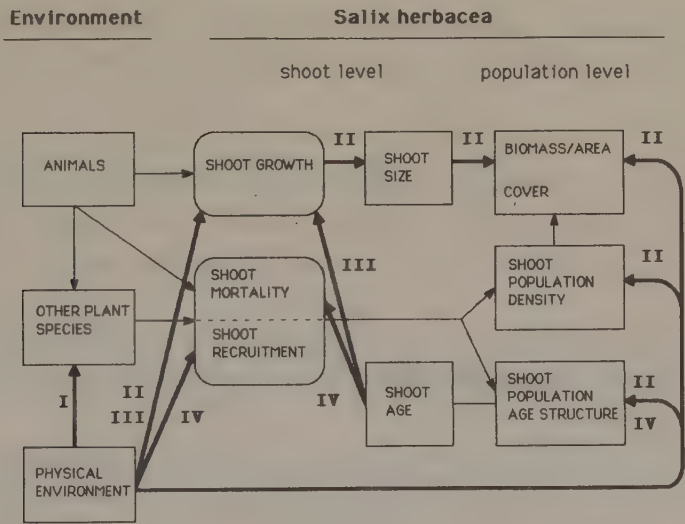


FIG. 1. A schematic survey of the interrelationships between the performance, growth, and shoot population dynamics of *Salix herbacea* and its environment. Bold arrows show the relationships studied in this thesis and the Roman numerals refer to the relevant papers.

ALPINE GRADIENTS OF SNOW COVER AND THE DISTRIBUTIONS OF VASCULAR PLANT SPECIES

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SUMMARY

(1) The distributions of vascular plant species were recorded in eleven transects along snow-cover gradients. Characteristic distribution curves were calculated, both in relation to snow duration and to a weighted-average ordination axis.

(2) Most species varied greatly in abundance between transects, but their peak abundance generally occurred within a specific interval of the gradient. However, a few species were distributed independently of the gradient.

(3) Altogether, the species distribution curves formed a vegetational continuum. However, there was a conspicuous boundary between *Vaccinium myrtillus* and *Salix herbacea* in all transects, suggesting strong competition between the two species.

(4) The date of snowmelt was a poor predictor of species distributions; most species probably respond to several other factors that vary within and among transects.

INTRODUCTION

The distribution of snow cover in alpine areas is mainly a function of wind and topography. Ridgetops usually have a shallow cover or remain exposed during winter, while several meters of snow can accumulate in depressions. Thus leeward slopes often show steep gradients in the depth and duration of snow cover.

The snow-bed gradients in the Scandinavian mountain range are associated with characteristic zonations in the vegetation, particularly in the low-alpine heath. This relationship was first pointed out by Vestergren (1902) and has since attracted much attention among phytosociologists (Fries 1913, Nordhagen 1928, 1943, Hedberg et al. 1952, Dahl 1956 and Gjørevoll 1956). Most works essentially agreed with the classification of Vestergren (1902), which emphasized the boundary between the *Vaccinium myrtillus* -heath and the grass communities below. For instance, Gjørevoll (1956) claims that it is "one of the most sharp-cut boundaries found between plant communities in the mountains".

Snow duration and length of the growing season are considered to be primary factors controlling the distribution of vegetation in snow cover gradients (Vestergren 1902, Fries 1913 p. 212, Tengwall 1920 p. 394, 1925 p. 716, Nordhagen 1928, Gjørevoll 1956). However, the few studies which actually included snow recession measurements of any significance related this factor to community distribution (Fries 1925, Gjørevoll 1949, Dahl 1956); therefore, the conclusions made regarding the distribution of individual species are not very well-founded. In addition to snow cover, several other factors have been considered important in this complex gradient, e.g. soil moisture, nutrient availability, and solifluction (Fries 1913, Hedberg et al. 1952, Dahl 1956, Billings 1974, Oberbauer and Miller 1979, Oberbauer and Billings 1981, Miller 1982).

This study examines the distribution patterns of vascular plant species along gradients of snow duration using the approach of direct gradient analysis (Whittaker 1967). The main objectives were to infer the importance of snow duration for species distributions, and to interpret the distribution pattern with respect to continuity and curve form.

MATERIALS AND METHODS

Study site and field methods.

The study area was situated above the tree-line (altitude 600 - 700 m) on the northern slopes of Mt. Vassitjåkka (68° 25' N, 18° 15' E), 15 km west of Lake Torneträsk in northern Sweden. The area has a cool oceanic climate with prevailing westerly winds, a mean annual temperature of - 1.4 °C and an annual precipitation of 807 mm (SMHI 1979). The topography is characterized by glaciofluvial terraces and ridges.

Belt transects, 1.0 m wide and of varying length, were laid out along eleven slopes. The slopes represented steep, long, and continuous snow duration gradients, and most of them had leeward (northerly or easterly) aspects (Table 1). Slopes with an uneven surface,

boulders, or eroded areas were avoided. The transects were deliberately positioned to include the vegetational shift between "*Vaccinium myrtillus* -heath" and "grass communities poor in calciphiles" according to the classification of Gjærevoll and Bringer (1965). However, *V. myrtillus* was very sparse in transect T-III and absent from T-IX. Positions within transects are given throughout this paper as distances from the top of each slope.

Snowmelt was monitored in T-I during 1978 - 80 and in all transects during 1981 - 83. From early June, records were collected on the position of the snow margin and the depth of the remaining snow, first weekly and later at shorter intervals. In addition, snowmelt data for the periods between field observations were obtained from near-ground air temperatures which were continuously recorded at several positions in transects T-I and T-V. In some of the transects melt-back had begun before the first measurement date in 1981 and 1983 (i.e. 7 June and 28 May, respectively). The snow release dates for the upper 0.5 - 1.5 m of these transects were estimated by assuming a 2 - 3 cm daily decrease in snow depth, which was the snowmelt rate observed in T-I during the period between 13 May and 7 June in 1981.

Soil sampling was carried out in T-I during 1980 and in the other transects during 1984. Six samples were collected at 1 - 3 m intervals along each transect, increasing the length of the interval towards the lower part of the transect. The thickness of the organic horizon and the soil pH were measured for each sample.

TABLE 1. Transect lengths, aspects, total number of vascular plant species, and number of species included in the study (within brackets).

Transect No.	Length (m)	Aspect	No. vascular plant spp.
I	14	69° N	21 (13)
II	7	79° E	21 (17)
III	12	87° E	26 (18)
IV	7	91° E	20 (16)
V	7	311° NW	17 (13)
VI	6	46° NE	35 (16)
VII	7	325° NW	18 (14)
VIII	8	70° E	15 (13)
IX	7	93° E	27 (18)
X	9	115° SE	23 (19)
XI	8	50° NE	20 (16)

The vegetation along the transects was sampled in August of 1977, 1978, and 1979, by recording the presence of vascular plant species in each 1dm². In the subsequent calculations, the abundance of each species was expressed as the accumulated frequency (F_i) within 0.5 x 1.0 m contiguous quadrats (i.e., $0 \leq F_i \leq 50$). The analyses included the 19 most frequent species; nomenclature follows that of Lid (1979).

Data treatment.

The data treatment aimed at combining the distributions in the eleven transects into a "median" distribution for each species in relation to: 1) time of snow release and 2) an ordination axis based on the vegetational composition. This was obtained by classifying the quadrats of a transect according to their average time of snow release and according to their

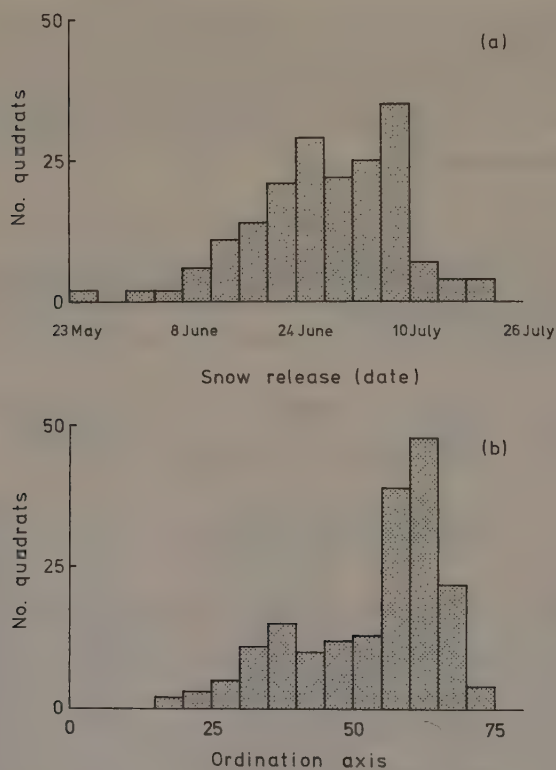


FIG. 1. Frequency distributions of quadrats according to the classifications of (a) snow duration, and (b) ordination scores. $n = 184$.

ordination scores (Fig. 1). The mean frequency, $\bar{F}_{ij}$, of species i in the quadrats belonging to class j was then calculated. Interpolation was occasionally used to estimate $\bar{F}_{ij}$ where there was a step over two class limits between successive quadrats. Finally, the median distributions were obtained as the median values of $\bar{F}_{ij}$ for all transects in which the species occurred. Extreme classes were pooled to represent a minimum of five quadrats.

Estimates of the goodness of fit between the abundance of each species in transect quadrats and these median distributions, c^2 , were calculated using a method analogous to that used for calculating the coefficient of determination, r^2 , in regression;

$$c^2 = 1 - \text{SS deviations} / \text{SS total}$$

where SS deviations is the sum of squared deviations from the expected frequencies (median $\bar{F}_{ij}$), and SS total is the sum of squared deviations from the grand mean of all quadrats (i.e. excluding transects in which the species was absent). By partitioning the sum of squares, c^2 was also calculated for individual transects.

The ordination of quadrats on a single axis was carried out using a weighted average technique (Ellenberg 1948, Whittaker 1967). The species were ranked according to the order in which their median of distribution appeared from the upper to the lower end in each transect. These rank orders were standardized to relative rank orders (RR) ranging between 0-100.

$$RR = \frac{(\text{Rank order} - 1)}{(\text{No. of species} - 1)} \times 100$$

The median value of the relative rank orders of all transects (MRR) was used as the species weight in the ordination. The quadrats were then ordinated according to the weighted average of the square roots of the species frequencies.

$$\text{ordination score} = \frac{\sum(\sqrt{F_i} \times MRR_i)}{\sum(\sqrt{F_i})}$$

Thus the ordination scores of quadrats have a theoretical range between 0 - 100. This method makes it possible to compare transects and species distributions on a common, easily interpretable gradient axis based purely on plant composition. However, a circularity is introduced since species distributions are not independent from the ordination axis. To estimate the degree of circularity, median distributions and the corresponding c^2 for *V. myrtillus* and *S. herbacea* were also calculated from ordinations where the species concerned had been excluded.

On several slopes, the major distributions of *Betula nana*, *Empetrum hermaphroditum*, and *Vaccinium vitis-idaea* were above the upper end of the transects. In such cases, the species were assigned the lowest rank order even when isolated plants occurred lower down in the transects. Species that occurred in just one quadrat in a transect where they had a frequency of less than 5 were omitted from the ranking.

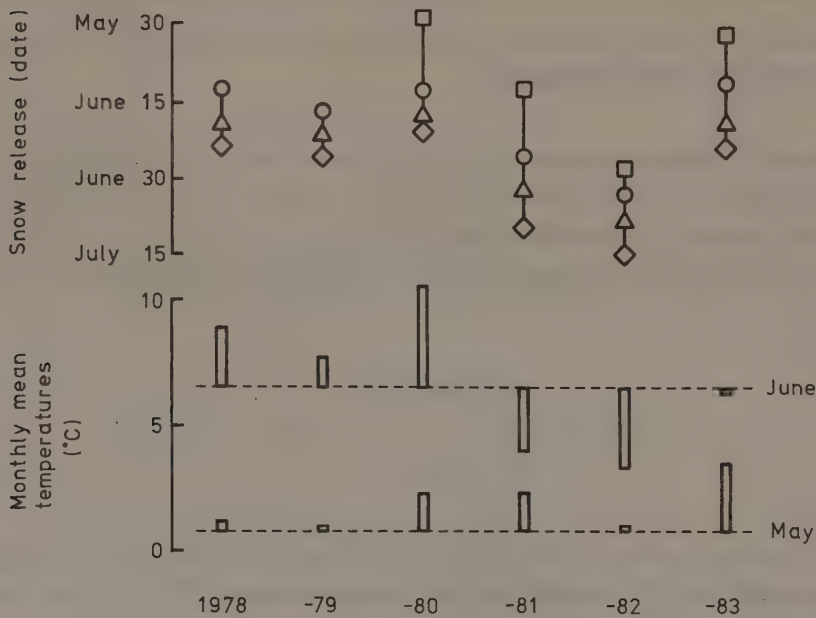


FIG. 2. Snow duration along transect T I and mean temperatures for May and June 1978 - 83. Snow release dates are shown for four sites along the transect: 4.0 m (□) (no data from 1978 - 79); 6.0 m (○); 8.0 m (△) and 14.0 m (◇). Mean temperatures at Katterjåkk are presented as deviations from the 1931 - 60 period average (data from Katterjåkk Meteorological Station, 5 km west of the study site).

RESULTS

Abiotic environment.

Snow duration and melting rates varied greatly between years and appeared to be closely related to the temperatures during May and June (Figs. 2 and 3). In 1982, June was cold and most of the transects were entirely covered with snow until late in the month. However, thereafter snowmelt proceeded rapidly and was completed 2 - 3 weeks later. In 1983, May temperatures were high and the upper and lower parts of the transects became snow-free about one month and 2 - 3 weeks earlier than in 1982, respectively. The May temperatures during 1981 were also above average and caused an early start in melt-back, but since June was cold, the duration of snow cover in 1981 ended up intermediate between that of 1982 and 1983.

The soil pH generally varied between 4.2 - 5.0. It increased in most transects by ca. 0.5 units from the upper to the lower end, but within T-III and T-XI it increased by only 0.2 units, (4.7 - 4.9). The lower section of T-VI differed markedly with a pH of 6.3. The increase in pH was associated with a decrease in the thickness of the organic horizon from between 2 - 6 cm at the upper end to typically less than 1 cm at the lower end.

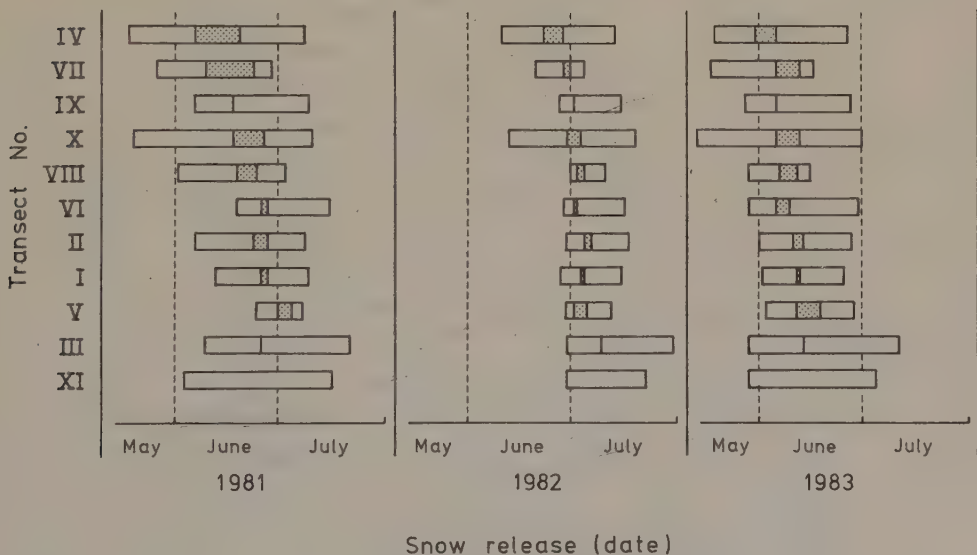


FIG. 3. Snow duration in the transects, 1981 - 83. The horizontal bars show the range in melt-back dates between the upper and lower ends of the transects. The shaded areas show positions of overlap between the upper *Salix herbacea* and the lower *Vaccinium myrtillus* distribution limits.

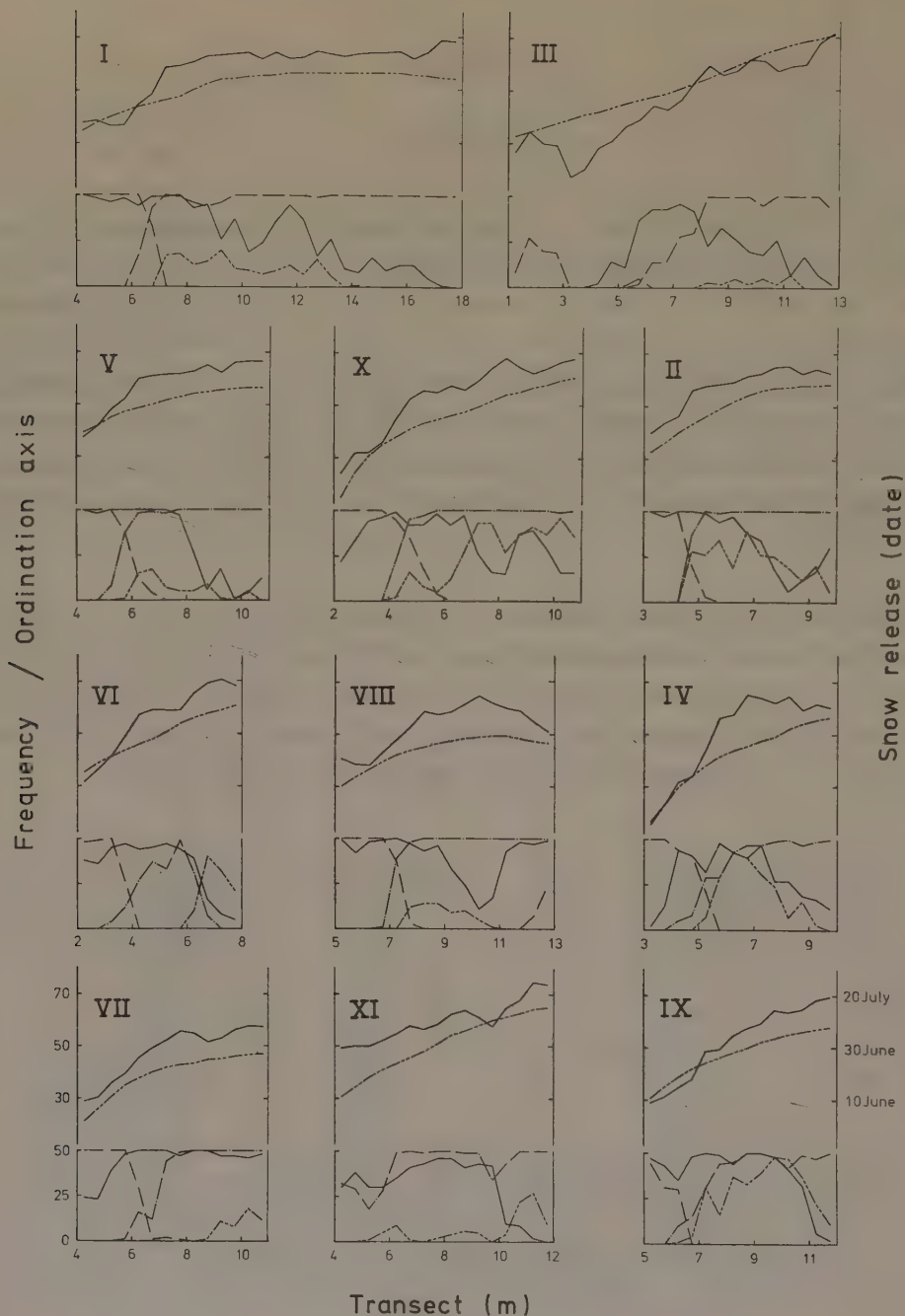


FIG. 4. Average snow release dates between 1981 - 83 (— — —), ordination axis values (———), and species distribution curves for, *Vaccinium myrtillus* (— · —), *Deschampsia flexuosa* (———), *Salix herbacea* (— · —) and *Anthoxanthum odoratum* (— · —). Species frequencies represent the occurrence in 1 dm² sub-quadrats within 0.5 m² contiguous quadrats.

Vegetation

The pattern of species distribution was similar in most transects as exemplified by the four species in Fig. 4. *Vaccinium myrtillus* and *Salix herbacea* were generally separated by sharp borders with only minor overlap. *Deschampsia flexuosa* reached maximal frequencies at these borders, while *Anthoxanthum odoratum* usually occurred in areas below the lower *V. myrtillus* limit. The similarities between distribution patterns were also evident by comparing the relative rank orders of species distribution centres along the various transects (Fig. 5). The rank order was fairly constant among the species at the upper end of the gradient, while there was more variation among transects for some of the species lower down. The changes in species composition were also greatest in the upper part of the transects. The ordination scores first increased rapidly down the transects and then levelled off (Fig. 4). The ordination scores ranged between 16.8 - 74.6, but almost half of the quadrats had values between 55.0 - 64.9 (Fig. 1).

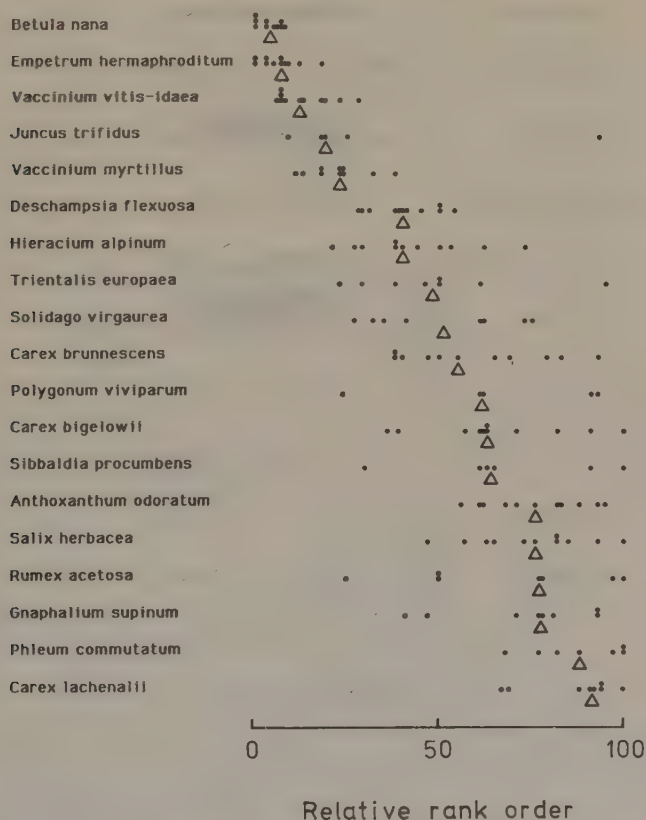


FIG. 5. Relative rank order of each species' median of distribution in each transect (dots) and median for all transects (Δ).

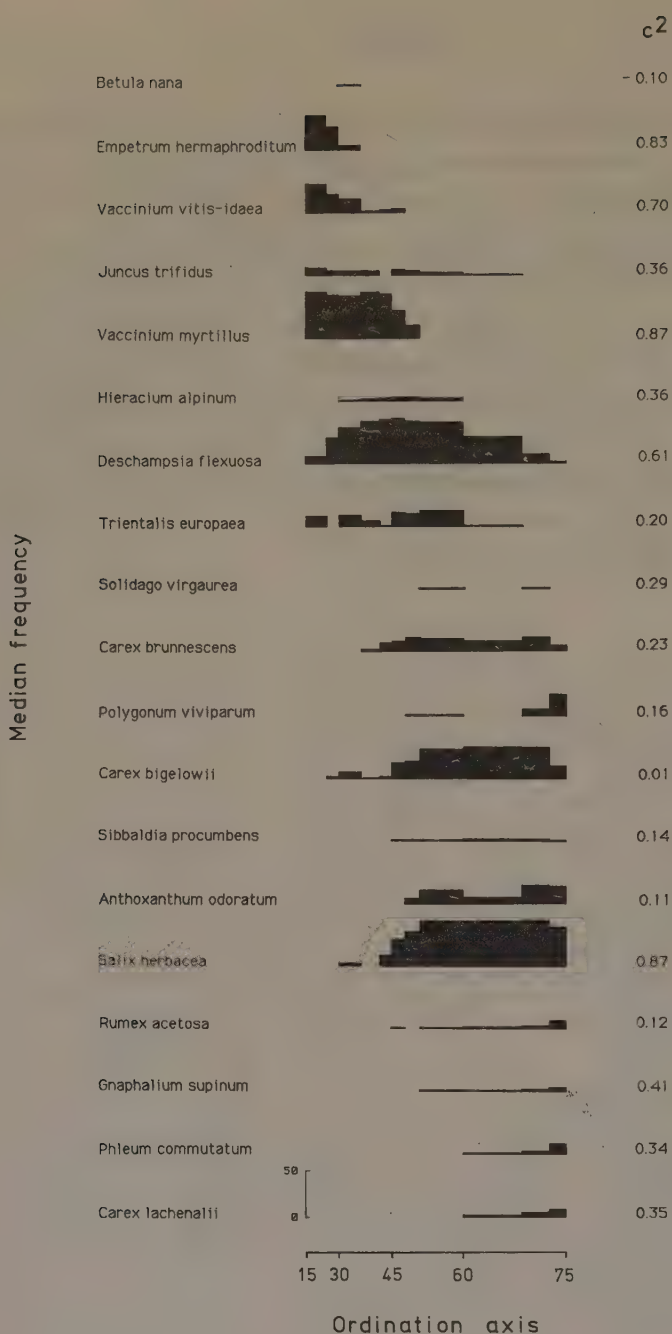


FIG. 6. Median distributions for each species related to the ordination axis. The abscissa intervals are proportional to the number of quadrats in each ordination score class. The goodness of fits are indicated as the median c^2 for all transects.

The median frequencies within ordination score classes represent the characteristic species zonation along the gradient. For 13 of the 19 species, the median distributions accounted for $\geq 20\%$ of the total variation (i.e. sum of squares) in more than half the number of transects (Fig. 6). Altogether, the "median transect" of ordination accounted for 37% of the variation in species frequencies. When *S. herbacea* and *V. myrtillus* were excluded from the ordination procedure, the c^2 values decreased from 0.87 for both species to 0.71 and 0.72, respectively.

The correlation between species distributions and average snow duration was weak (Fig. 7).

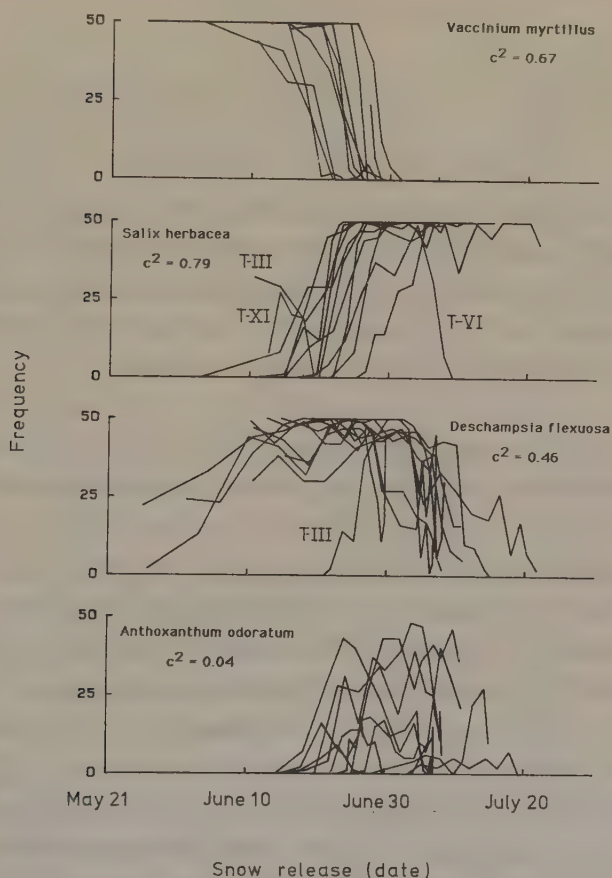


FIG. 7. Species distribution curves for all transects related to the 1981-83 average snow release dates. Transect numbers are indicated for deviating curves. c^2 indicates the goodness of fit between original transect data and median distribution for each species.

TABLE 2. Variation among transects in the duration of snow cover at species distribution limits (1981 - 83 average).

	Transect average	± s.d. (days)	Range (days)
<i>Salix herbacea</i> , upper	19 June	5	15
<i>Vaccinium vitis-idaea</i> , lower	21 June	8	28
<i>Vaccinium myrtillus</i> , lower	24 June	4	12
<i>Anthoxanthum odoratum</i> , upper	26 June	7	18
<i>Sibbaldia procumbens</i> , upper	28 June	8	20
<i>Gnaphalium supinum</i> , upper	29 June	6	18
<i>Carex lachenalii</i> , upper	1 July	7	21
<i>Hieracium alpinum</i> , lower	5 July	7	23
<i>Phleum commutatum</i> , upper	6 July	7	19

Snow duration at the species distribution limits differed by 2 - 3 weeks among transects (Table 2), and specific melt-back dates corresponded to very different ordination scores in different transects (Fig. 4). The median distributions obtained from the snowmelt classification accounted for 27% of the total variation, and for 9 of the 19 species, $\geq 20\%$ of the variation was accounted for in more than half of the transects.

Although the transects were very similar, there were some deviations from the typical pattern of species distributions due to the specific characteristics of certain transects.

V. myrtillus was absent from T-XI and occurred in only 6 dm² in T-III. The species composition in these transects was otherwise similar to that of the other transects (Fig. 4). In T-III and T-XI, *S. herbacea* was abundant in areas with melt-back dates which, in other transects, usually occurred well above the upper distribution limit for the species (Fig. 7). The upper part of T-XI had high ordination scores in relation to melt-back dates while T-III had very low scores due to the high abundance of *Empetrum hermaphroditum*.

In T-VI, the section below 6 - 7 m was evidently affected by calcareous soil causing a considerable pH increase. Here, *S. herbacea* was replaced by *S. polaris*, and many calciphiles occurred that were absent in all other transects, e.g., *Cerastium cerastoides*, *Arabis alpina*, *Ranunculus nivalis*, and *Sagina saginoides*. *Deschampsia flexuosa*, *C. bigelowii* and several other species showed a sharp decrease in the calcareous section and this vegetational shift resulted in an abrupt increase in ordination scores (Fig. 4).

In T-VIII, snow-depth and melt-back dates decreased in both directions from the middle of the transect, which explains why *V. myrtillus* and *D. flexuosa* increased their frequencies towards the lower end of the transect (Fig. 4).

In T-X, a reindeer track crossed the transect at about 8.0 m. In this region there were decreased frequencies of *D. flexuosa* and *Anthoxanthum odoratum* (Fig. 4), while *Gnaphalium supinum*, *Sibbaldia procumbens*, and *Agrostis tenuis* reached local maxima. The track appears as a marked peak in the ordination scores.

DISCUSSION

The vegetational gradient.

Evidently, zonation of the vegetation did occur along the gradient, and the ranking procedure effectively separated the species spectra (Fig. 5). The considerable variation in the rank order of some species was probably due to the large overlaps in distributions that occurred particularly in the lower end of transects. However, most species still showed their highest abundance within specific intervals of the gradient. Thus even *Deschampsia flexuosa* (with the widest amplitude of all species) showed a narrow range of rank orders. However, there were a few species, such as *Carex bigelowii* and *Juncus trifidus*, which seemed to be distributed independently of the gradient. For *C. bigelowii* this independence was also reflected by a poor fit to the median distribution (median $c^2 = 0.01$).

However, low c^2 -values are mainly caused by high variations in abundance among transects, not by variations in the distribution relative to the gradient (cf. *Anthoxanthum odoratum*, Fig. 4). This is probably true for the majority of species which likely responds to several factors in addition to those that vary along the gradient. The best fits with median distributions were found in species that reached high levels of abundance in the majority of transects, i.e. *Empetrum hermaphroditum*, *V. myrtillus*, *D. flexuosa*, and *S. herbacea*, implying that they were primarily responding to the main gradient. It could be argued that the median distribution for a species is not independent from the ordination axis. However, exclusion of a species from the ordination only caused minor reductions in its c^2 -value. Also, the distribution patterns were not seriously affected by this circularity since the ordinated sequence of quadrats remained essentially the same as that in the field transects (Fig. 4, cf. Whittaker 1956, 1967).

Continuity and form of distribution curves.

The species distribution pattern argues against the existence of any distinct community boundaries, and the changes in ordination scores along the transects generally form smooth curves except for minor discontinuities (some of these are explained in the results section). Thus the snow cover gradient in this study appears to be a good example of a vegetational continuum. The lower distribution limit of *V. myrtillus* was very conspicuous and coincided closely with the upper limit of *S. herbacea*; however, since the remaining species were distributed independently of this boundary, there is no evidence for a community boundary. The coinciding distribution limits of the two species are most likely a result of competition (Wijk 1986).

The sharp boundaries between *V. myrtillus* and *S. herbacea* are somewhat blurred in the diagrams due to interpolations (i.e. Figs. 4, 6 and 7). The use of direct gradient analysis made it apparent here that interpolations and averages smooth curves and disguises sharp limits; however, this may easily be overlooked when using indirect gradient analysis i.e.

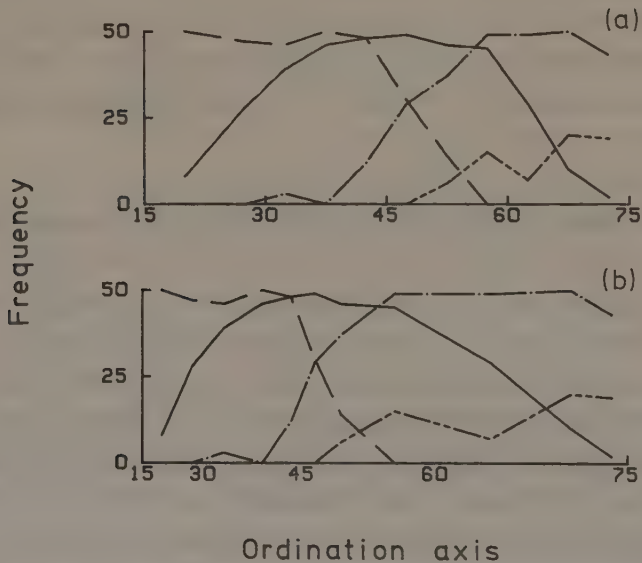


FIG. 8. The effect of the abscissa scale on the form of species median distribution curves: (a) linear scale; (b) transformed scale where each interval length along the x-axis is proportional to the number of quadrats it represents.

ordination methods with random sampling, or when using discontinuous or composite transects (cf. Whittaker 1967). It follows that "Gaussian" (bell-shaped) distribution curves may often be artifacts of the methods, and that sharp distribution limits may be more common than generally believed. The form of distribution curves also depends on the scale used for the environmental gradient (Austin 1976). Fig. 8 shows the median distributions for four species in relation to both the ordination axis directly and to the same axis when the size of each interval is proportional to the number of quadrats it actually represents. The latter scale is more consistent with reality (cf. Fig. 4), while the former tends to form bell-shaped curves.

The importance of snow duration.

Undoubtedly, snow depth plays a significant role in determining vegetation distributions in alpine areas, protecting plants from extremely low temperatures and the abrasive action of wind (Dahl 1956, Sonesson 1969, Bell and Bliss 1979). Several studies have also shown that prolonged snow cover can reduce plant growth (Billings and Bliss 1959, Knight et. al. 1977, Wijk 1986) and there is probably a minimum length of growing season below which a species can no longer retain a positive carbon balance. However, there is no evidence that growing season length is a crucial factor affecting species distributions in low alpine areas with relatively moderate snow depths. On the contrary, my results show that species distributions vary considerably among transects with respect to time of snow release (Table 2, Fig. 7). An extended observation period would probably not improve the relationship, since the melt-back order between distribution limits in different transects remained essentially the same from year to year. In addition, the differences in snow duration within the transects appear to be minor compared with the great variation among years (Fig. 2 and 3, Fries 1925, Billings and Bliss 1959, Flock 1978).

It could be argued that the distribution pattern is due to vegetation damage occurring in certain years with extremely late snowmelt (Resvoll-Holmsen 1920 and Dahl 1956). Recovery after such events could take many years because of slow colonisation processes. However, there was no visual damage following 1982, which was extreme with respect to early summer temperatures and snow release dates (Fig. 2). Also, the differences in snow duration within transects are likely to be less in years with late snowmelt.

The species distribution pattern within the gradient cannot be explained by the snow duration factor alone, but is more likely related to several factors, possibly different for each species. The species which are usually restricted to the upper part of the gradient are plants with woody structures which make them more susceptible to mechanical damage caused by snow pressure and solifluction. Vestergren (1902 p. 246) suggested that snow pressure could be partly responsible for the lower distribution limits of *Betula nana* and *Empetrum hermaphroditum*, and the presence of considerable lateral forces under deep snow has been demonstrated by Costin et al. (1973). In general, these woody species are also associated with stable soils with a well developed organic horizon that prevents solifluction (Dahl 1956). Water-logging during snowmelt could be detrimental to some species, particularly *V. myrtillus* (cf. Hedberg et al. 1952, Anderson 1961). On the other hand, some species restricted to the lower part of the transect are abundant in meadow vegetation and are most likely dependent on seasonal irrigation or high water tables in summer, i.e. *Anthoxanthum odoratum*, *Sibbaldia procumbens*, *Rumex acetosa*, *Polygonum viviparum*, and *Phleum commutatum*. Finally, there is a group of species abundant in the middle of the gradient which shows a decline along the gradient as snow duration becomes shorter, i.e. *Hieracium alpinum*, *Deschampsia flexuosa*, *Trientalis europaea*, *Solidago virgaurea*, *Carex bigelowii*, *C. brunnescens*, and *Salix herbacea*. These species are probably physiologically capable of growing higher up in the transects but are suppressed by competition with other plants, especially the dominating dwarf shrubs (Dahl 1956, Knight et al 1977, Wijk 1986).

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REFERENCES

- Anderson, D.J. (1961).** The structure of some upland plant communities in Caernarvonshire. II. The pattern shown by *Vaccinium myrtillus* and *Calluna vulgaris*. - *Journal of Ecology* 49: 731-738.
- Austin, M.P. (1976).** On non-linear response models in ordination. - *Vegetatio* 33: 33-41.
- Bell, K.L. and Bliss, L.C. (1979).** Autecology of *Kobresia bellardii*: Why winter snow accumulation limits local distribution. - *Ecological Monographs* 49: 377-402.
- Billings, W.D. (1974).** Arctic and alpine vegetation: plant adaptations to cold summer climates. - In: Ives, J.D. and Barry, R.G. (eds.) *Arctic and alpine environments*. Methuen, London. pp. 403-443.
- Billings, W.D. and Bliss, L.C. (1959).** An alpine snowbank environment and its effect on vegetation, plant development and productivity. - *Ecology* 40:388-397.
- Costin, A.B., Jennings, J.N., Bautovich, B.C. and Wimbush, D.J. (1973).** Forces developed by snowpatch action, Mt. Twyman, Snowy Mountains, Australia. - *Arctic and alpine research* 5: 121-126.
- Dahl, E. (1956).** Rondane - mountain vegetation in South Norway and its relation to the environment. - *Det Norske Videnskabs-akademi i Oslo. I. Mat.-Naturv. Klasse.* 1956. No. 3. Oslo.
- Ellenberg, H. (1948).** Unkrautgesellschaften als mass für den säuregrad, die verdichtung und anderer eigenschaften des Ackerbodens. - *Bericht über Landtechnik* 4: 130-146.
- Flock, J.W. (1978).** Lichen bryophyte distribution along a snow-cover soil-moisture gradient, Niwot ridge, Colorado. - *Arctic and Alpine Research* 10(1): 31-47.
- Fries, Th.C.E. (1913).** Botanische undersøkelungen im nördlichsten Schweden. - *Dissertation. Uppsala.* 361 pp.
- Fries, Th.C.E. (1925).** Ökologiske und phänologiske beoektelungen bei Abisko in den Jahren 1917 - 1919. I. - *Svenska Växtsociologiske Sällskapet's Handlingar* V. Uppsala. 171 pp.
- Gjørevoll, O. (1949).** Snøleievegetasjonen i Oviksfjellene. (The snow-bed vegetation of Mts Oviksfj., Jämtland, Sweden). - *Acta Phytogeographica Suecica* 25. Uppsala
- Gjørevoll, O. (1956).** The plant communities of the Scandinavian alpine snow-beds. - *Det Kunglige Norske videnskabers selskabs skrifter.* Trondheim. 405 pp.
- Gjørevoll, O. and Bringer, K-G. (1965).** Plant cover of the alpine regions. - *Acta Phytogeographica Suecica* 50: 257-268.
- Hedberg, O., Mårtensson, O. and Rudberg, S. (1952).** Botanical investigations in the Pältsa region of northernmost Sweden. - *Botaniska Notiser Supplement* 3(2). 209 pp.
- Knight, D.H., Rogers, B.R. and Kyte, C.R. (1977).** Understorey plant growth in relation to snow duration in Wyoming subalpine forest. - *Bulletin of the Torrey Botanical Club* 104:314-319.
- Lid, J. (1979).** Norsk og svensk flora. 2nd ed. Det norske samlaget. Oslo. 808 pp.
- Miller, P.C. (1982).** Environmental and vegetational variation across a snow accumulation area in montane tundra in central Alaska. - *Holarctic Ecology* 5:85-98.
- Nordhagen, R. (1928).** Die flora und vegetation des Sylengebietetes. - *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. I. Mat.-Naturv. Klasse* 1927. No. 1. 612 pp. Oslo.
- Nordhagen, R. (1943).** Sikilsdalen og Norges fjellbeiter. - *Bergens Museums Skrifter* 22. Bergen. 607 pp.
- Oberbauer, S.F. and Billings, W.D. (1981).** Drought tolerance and water use by plants along an alpine topographic gradient. - *Oecologia* 50: 325-331.
- Oberbauer, S.F. and Miller, P.C. (1979).** Plant water relations in montane and tussock tundra vegetation types in Alaska. - *Arctic and Alpine Research* 11(1):69 - 81.
- Resvoll-Holmsen, H. (1920).** Om fjeldvegetationen i den østenfjeldske Norge. - *Archiv f. Math. og Naturv.* Bd 37. 266 pp.

- SMHI (1979).** Månadsöversikt över väderlek och vattentillgång. (Monthly and yearly summary of wheather and water supply in Sweden.) Yearbook, Vol. 61. Sveriges meteorologiska och hydrologiska institut. Stockholm.
- Sonesson, M. (1969).** Studies on mire vegetation in the Torneträsk area, Northern Sweden. II. Winter conditions of the poor mires. - Botaniska Notiser 122: 481-511.
- Tengwall, T.Å. (1920).** Die vegetation des Sarekgebietes. I. - Naturwissenschaftliche untersuchungen des Sarekgebirges in Schwedisch-Lappland. Bd III: 269-435.
- Tengwall, T.Å. (1925).** Die vegetation des Sarekgebietes. II. - Naturwissenschaftliche untersuchungen des Sarekgebirges in Schwedisch-Lappland. Bd III: 704-774.
- Vestergren, T. (1902).** Om den olikformiga snöbetäckningens inflytande på vegetationen i Sarjekfjällen. - Botaniska Notiser 1902 pp.241-268.
- Whittaker, R.H. (1956).** Vegetation of the Great Smoky Mountains. - Ecological Monographs 26:1-80.
- Whittaker, R.H. (1967).** Gradient analysis of vegetation. Biological reviews 42: 207-264.
- Wijk, S. (1986)** in press. Performance of *Salix herbacea* in an alpine snow-bed gradient. - Journal of Ecology 74.

PERFORMANCE OF *SALIX HERBACEA* IN AN ALPINE SNOW-BED GRADIENT

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SUMMARY

(1) Changes in percentage cover, biomass distribution, shoot growth, shoot density and shoot age distribution of the rhizomatous dwarf shrub *Salix herbacea* were studied along a belt transect which spanned a sharp gradient in snow cover.

(2) *S. herbacea* showed its maximum cover, biomass and shoot density in the lowermost section of the topographical gradient where snow persisted for the longest period. However, maxima in size and growth of individual shoots were found at the upper distributional limit. Low competitive ability might explain why this species is restricted to areas with severe climatic conditions.

(3) Lower average shoot age and absence of shoots over 10 years old in the upper part of the transect indicate a higher mortality rate, probably due to competitive stress and herbivore damage.

(4) Within the transect, a 20% increase in growing season length was associated with a five-fold increase in *S. herbacea* shoot growth. The great difference in growth is probably related to differences in plant and rhizome age-structures in addition to differences in length of the growing season.

INTRODUCTION

In alpine areas, the interaction between wind and topography causes a very irregular distribution of the winter snow. Snow accumulates in depressions where it can remain until late summer while nearby ridges may remain snow-free throughout the winter. Thus, there are often steep gradients of snow cover and snow duration along the hill slopes. Other factors such as microclimate, nutrient availability and soil moisture can also vary considerably along the same slopes. This complex abiotic gradient is generally associated with great differences in plant species composition within short distances (Gjaerevoll 1956; Knight, Rogers & Kyte 1977; Flock 1978; Miller 1982).

In the alpine regions of Scandinavia, *Salix herbacea** is one of the dominant vascular species in late-exposed, non-irrigated snow-bed communities on acid soils (Gjaerevoll 1956). This species also occurs on fellfields and in a wide range of other habitats, but it is generally absent from the *Vaccinium myrtillus* zone adjacent to the snow-bed communities (Gjaerevoll 1956). This restriction in the distribution of *S. herbacea* may be the result of its relatively low competitive ability or of maladaptation to the abiotic conditions. The aim of this work has been to determine what factors limit the distribution of *S. herbacea* by investigating how its performance changes along a snow cover gradient.

In general, prolonged snow cover restricts plant growth (Knight, Rogers & Kyte 1977; Billings & Bliss 1959). However, according to Gjaerevoll (1956), *S. herbacea* 'attains its maximum vigour and competing power' in late-exposed snow-beds. If this is the physiologically optimal environment for the species one would expect it to be associated with a

* Nomenclature for vascular plants follows Lid (1979).

growth rate maximum. However, if the restriction of *S. herbacea* to snow-beds is due to competitive exclusion from more favourable sites, then the growth rate should be expected to increase as snow cover decreases.

In the present paper, growth studies on *S. herbacea* focused on the above-ground parts and shoots were regarded as population units. Biomass distribution analyses were made to reveal any changes in the balance between above- and below-ground parts along the gradient. Because shoot density is important in the interpretation of growth measurements based on individual shoots (Callaghan & Collins 1981), this variable was also measured. The age distribution of shoots was also included in the study since it was a source of additional information about differences in environmental stress along the transect.

MATERIALS AND METHODS

Study site

Field work was carried out in an alpine snow-bed at an altitude of 600 m near Vassijaure (68°25'N, 18°15'E), 15 km west of Lake Torneträsk in the northernmost part of the Scandinavian mountain range. The region is regarded as having a maritime climate (Wallén 1948). The climatic station at Katterjåkk, 5 km west of the site, receives an average of 807 mm annual precipitation and has a mean annual temperature of -1.4°C . The coldest month is February, with a mean temperature of -11.2°C , and the warmest is July, with a mean of 11.3°C (SMHI 1979). At this latitude there are midnight-sun-conditions theoretically between 26 May and 18 July. However, surrounding mountains and local topography significantly reduce the maximum number of sunshine hours (Lindholm 1955).

A belt transect, 1 m wide and 18 m long, was positioned along the slope of a glacio-fluvial terrace representing a steep gradient in snow cover. All positions in the transect are stated in the following text as distances in metres from a zero position located on the ridge of the topographical gradient (Fig. 1a).

The *Empetrum hermaphroditum* heath in the fellfield at the top of the terrace is delimited by a narrow zone of *Betula nana* shrubs (0–1.5 m, Fig. 1d). Below this shrub border is a zone (1.5–7 m) dominated by *Vaccinium myrtillus* and locally, *Juncus trifidus*. In the snow-bed vegetation (7–15 m), there is a gradual shift in dominant species from *Deschampsia flexuosa* at the upper end to *Salix herbacea* and *Carex bigelowii* at the lower end. The part of the transect below 15.0 m is waterlogged during snow melt and hydrophilous species such as *Juncus arcuatus* and *Equisetum palustre* are abundant. There is also a zonation in the ground layer with *Stereocaulon paschale* and *Cladonia* species predominant in the *V. myrtillus* zone while *Dicranum* spp., *Polytrichum* spp. and liverworts are the most common species in the snow-bed. This zonation of the vegetation coincides with the general pattern for low-alpine heath communities poor in calciphiles (Gjaerevoll & Bringer 1965).

The soil profile is podsollic in the *Vaccinium*-zone, but poorly developed in the lower parts of the snow-bed where a thin humus layer rests directly on the mineral soil which is a moraine with a high content of micaceous schist.

Snowmelt observations

The distribution of snow in the transect was measured monthly from October 1977 until June 1980. During the 1978–81 snow-melt-periods, more frequent observations were made in the field and data from field temperature measurements were also used for

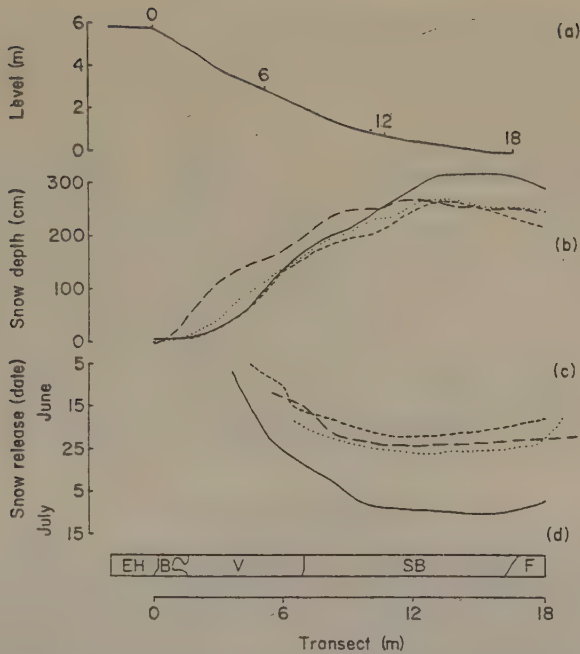


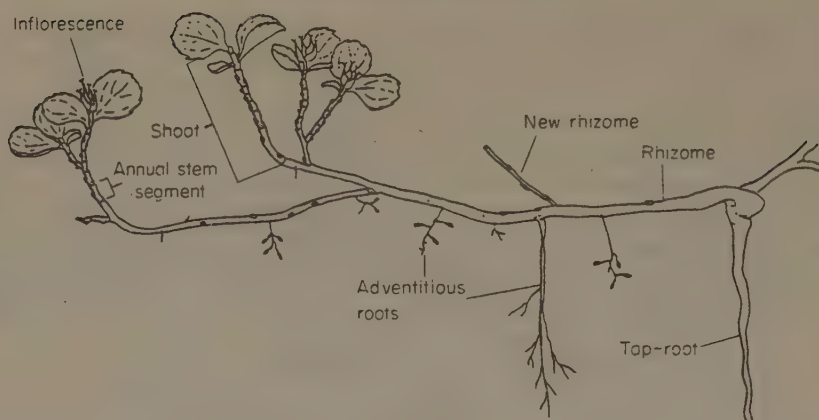
FIG. 1. Environmental characteristics of a transect along a snow-bed gradient in Sweden. (a) topography; (b) snow distribution before melting, late April–early May; (—), 1978; (.....), 1979; (-----), 1980; (—), 1981; (c) snow duration; (d) main vegetation zones: EH, *Empetrum hermaphroditum* heath; B, *Betula nana* shrubs; V, *Vaccinium myrtillus* heath; SB, snow-bed vegetation; F, fen.

dating snow release. Temperatures were recorded every hour from thermistors placed 2 cm above the ground surface at 2-m intervals along the transect. The date of snow release was readily identified since it coincided with an immediate rise in temperature above freezing-point.

Plant cover and phenology

Vegetation analyses within the transect were carried out in August 1977 using a 1.0-m² quadrat subdivided into 1-dm² squares. The ground cover of *S. herbacea* was estimated in each of the subquadrats according to a five-grade logarithmic scale with the upper class limits of $\frac{1}{1}$, $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$ and $\frac{1}{16}$. An estimate of percentage cover for each 0.5 m section of the transect was calculated as the average of the mid-class percentages for the 50 subquadrats. Presence or absence of all vascular plant species were recorded in each subquadrat and frequencies were calculated for each 0.5 m section.

The phenology of *S. herbacea* was monitored in five observation plots in 1980. Each observation plot comprised 400 cm² and leaf area was determined using a 0.25 cm² grid net on a transparent sheet was attached to the vegetation. The extent of bud-break and subsequent leaf expansion were noted every fourth day during June, followed by two observations in July and one in August.

FIG. 2. Morphology of *Salix herbacea*.

Salix herbacea morphology

Salix herbacea is a dioecious dwarf-shrub with an extensive ramifying system of rhizomes, and plant individuals are difficult to distinguish in the field. However, when excavated, most rhizomes can be traced back to a thick tap-root (Fig. 2). The rhizome branches continue into aerial shoots which usually extend only a few centimetres above ground. The bud scales of the shoot apices leave encircling scars. Thus, the stem becomes distinctly segmented where each segment corresponds to the annual increment in length (Resvoll 1917; Sørensson 1941). This characteristic has previously been used to determine the age of *Salix* shoots in glacial research (Palmer & Miller 1961). Adventitious roots sometimes occur on shoot segments embedded in the ground and this makes the strict division between shoots and rhizomes somewhat arbitrary.

Shoot sampling

Shoots were sampled in late August 1977, at 0.5–2.0-m intervals along the transect. At each sample site a string was fitted at right angles to the transect and all shoots crossing the string were cut at rhizome level. Shoots within 10 cm of each edge of the transect were excluded. On a few occasions, when fewer than thirty shoots occurred along the string, it was alternatively moved 2 cm upwards and downwards until the sample size exceeded thirty.

The ages of all shoots were determined by counting the number of annual stem-segment generations. Each shoot was then placed into one of three age groups representing 1–3, 4–6 and greater than 6 years of age (i.e. growing seasons). The shoots were cut into annual segments and those segments of equal age originating from the same age group of shoots and from the same sample site were pooled. Stem segments, leaves, apical buds and inflorescences were over-dried at 80 °C for approximately 24 h. Weight (± 0.1 mg) and length (± 0.5 mm) were measured for each segment separately. A relative estimate of shoot growth in each sample was made by summing the average lengths and weights for the segment generations produced during 1972–77. Shoots less than seven years old were not included. Thus, this 'accumulated growth' corresponds to the total size of the six most recent annual segments of an average shoot axis and does not include secondary growth in the older parts of the stems or rhizomes.

Biomass sampling

In late August 1978, 10 cm × 10 cm samples were removed from the ground at 1.0-m intervals within the transect between 6.8–17.8 m. Complementary sampling was carried out in 1980 at 6.5, 7.5, 9.0, 11.0, 14.0 and 17.0 m using 7.0 cm-diameter, 5.0 cm-deep cylinder cores. At each site six cores were systematically sampled. All *S. herbacea* structures not obviously decayed were regarded as biomass, and the shoots were counted and aged. The plant material was washed and divided into apical buds, leaves, current year's stem segments, remaining shoot stems, rhizomes and roots. Each fraction was separately oven-dried and weighed. Linear regressions were then calculated for each fraction using the angular transformation of the proportion of total biomass as the dependent variable and position in the transect as the independent variable. In these calculations, weight data from samples with a total biomass less than 1.0 g were combined with data from adjacent samples, i.e. 6.5 + 6.8 m, 7.5 + 7.8 m and 8.8 + 9.0 m. The regression coefficients were tested for significance using Student's *t*-test (Sokal & Rohlf 1969).

RESULTS

Length of the growing season

The depth and distribution of snow along the transect varied little between years (Fig. 1b). The snow release date at a particular transect level varied considerably between years (Fig. 1c). The greatest difference in melt-back dates was between 20 June (1980) and 10 July (1981) at the 16 m-level. The part of the transect where *S. herbacea* occurs was characterized by winter snow depths generally exceeding 2 m and with snow remaining until late June. Within this section melt-back dates differed by 8–14 days.

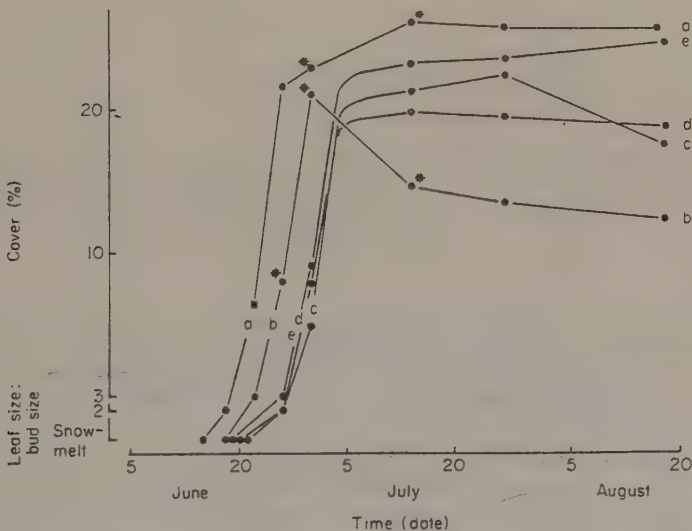


FIG. 3. Phenology of *Salix herbacea* along a snowmelt gradient in 1980. Leaf development during bud-break is expressed as categories of leaf size to bud size ratio (ratio = 2 or 3) and thereafter as percentage cover. The positions of the observation plots were: a, 7.1 m; b, 8.1 m; c, 10.2 m; d, 14.2 m and e, 16.8 m. Grazing on leaves occurred where indicated by asterisks.

In 1980, bud-break occurred rapidly after the snow cover had disappeared and, within two weeks, the leaf area reached at least 75% of the maximum value observed (Fig. 3). The rate of phenological development was essentially the same for all observation plots regardless of differences in snow release dates. Changes in leaf area later in the season were small except for grazing effects in some cases. Thus, consumption of buds and newly formed leaves by *Phytodecta affinis* Gyll. (Coleoptera: Chrysomelidae) caused locally severe damage. Occasionally, this led to the formation of new leaves later in season from dormant shoot buds.

The length of the growing season for *S. herbacea* in 1980 was 78 days at 7.1 m and 70 days at 10.2 m, if estimated as the period between 25% leaf expansion, i.e. 22 June and 30 June, respectively, and the end of season (defined as 7 September).

Because no field observations were made at the end of the growing season, the actual date was an estimate based on climatic records which showed that the first snowfalls and frosts occurred during the first half of September.

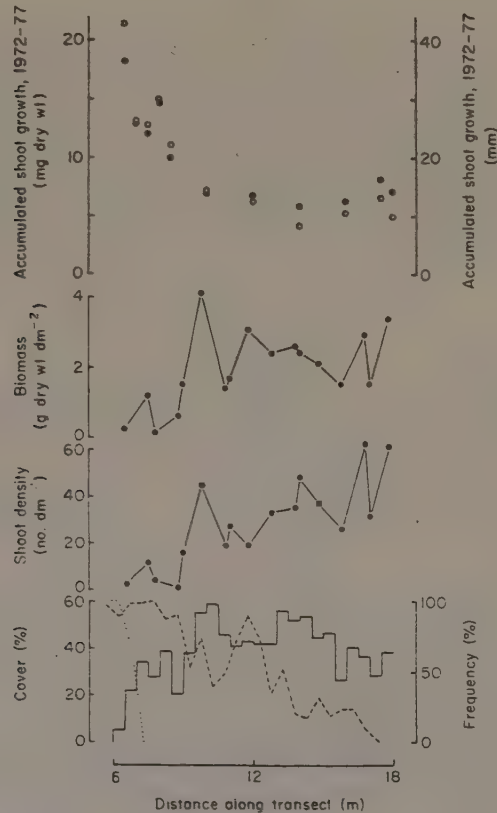


FIG. 4. Shoot growth, biomass, shoot density and cover of *Salix herbacea* along a snowmelt transect. Shoot growth is expressed as accumulated mean weight (open circles) and length (filled circles), respectively, of annual segments produced during 1972–77. The distribution curves of *Vaccinium myrtillus* (.....) and *Deschampsia flexuosa* (----) are also presented.

Cover, shoot density and biomass

The percentage cover of *S. herbacea* showed a sharp increase from its upper distribution limit at 6 m, down to about 10 m where the maximum was reached. Below this level there were no considerable changes except for a slight decrease at the lower end of the transect (Fig. 4). The distribution pattern of *S. herbacea* biomass per unit area was very similar to the cover pattern with a maximum at 9.8 m, a sharp decline towards the upper distribution limit and no clear tendency in the lower part of the transect. Shoot density showed a general increase down the transect, although minor fluctuations did occur and appeared to be associated with variation in cover and biomass.

Shoot growth

Accumulated shoot growth showed a sharp decrease down the transect except for a slight increase in the lowermost part (Fig. 4). Linear regression of the logarithm of the accumulated growth showed a significant positive relationship ($P < 0.05$) with the average snow release date. The linearity of the relationship was somewhat stronger for length data ($r^2 = 0.90$) than for weight data ($r^2 = 0.82$), (Fig. 5).

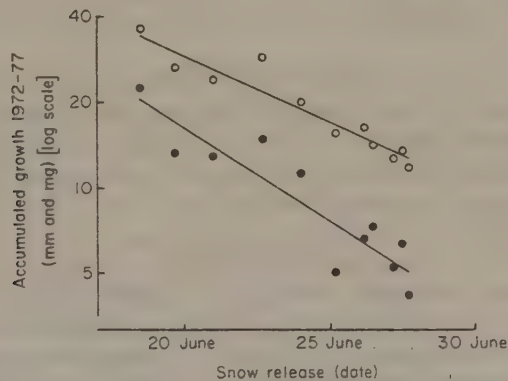


FIG. 5. Shoot growth of *Salix herbacea* in relation to length of the growing season. The logarithms of accumulated growth (same material as in Fig. 4) have been plotted against the date of snow release at the sample sites (averages for 1978-81) for positions along a snowmelt gradient. The lines are linear regressions of weight (filled circles), $r^2 = 0.82$ and length (open circles), $r^2 = 0.90$.

TABLE 1. Biomass distribution of *Salix herbacea* along a snow-bed gradient. Linear regressions were calculated for each fraction after angular transformation of percentage values using position along the transect as the independent variable.

Symbols: *, $P \leq 0.05$; **, $P < 0.01$; NS, not significant.

Fraction	Proportion of dry biomass		Linear regressions		n
	Median (%)	Range (%)	Coefficient	r^2	
Leaves	11	5-14	-0.51**	0.54	14
Apical buds	0.6	0-1	N.S.	0.05	13
Current year's segments	1.1	1-3	-0.21*	0.37	13
Shoot stems	16	11-34	N.S.	0.01	15
Rhizomes	59	41-73	N.S.	0.18	15
Roots	8	4-22	-0.85**	0.42	15

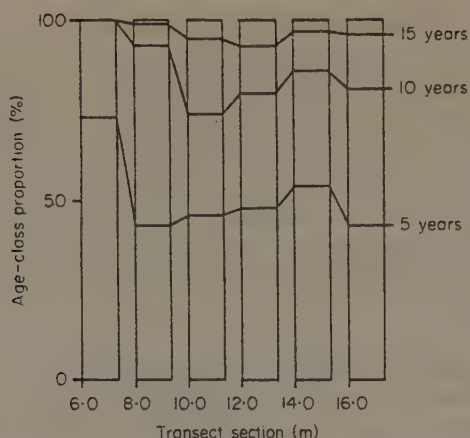
Performance of Salix herbacea

FIG. 6. Age distribution of shoots of *Salix herbacea* along a snowmelt transect. The proportions of shoots belonging to each of four age classes: 1-5, 6-10, 11-15 and >15 years old, are represented for each 2.0-m section of transect. Data from all available shoots included in string samples and biomass samples are incorporated.

Biomass distribution

The biomass distribution varied considerably between samples but no trend was found for the stem and rhizome fractions, which comprised about 75% of the total biomass. However, the proportions of current year's segments, leaves and roots all showed a significant decrease down the gradient (Table 1).

Age distribution

Shoot age distribution was similar throughout the gradient except for the uppermost part of the transect where the shoots were, on average, younger than in the population below (Fig. 6). Above 8.0 m only 27% of the shoots were older than five years compared with 47% below this level. Shoots older than ten years did not occur above 8.0 m and were most frequent below 10.0 m.

DISCUSSION

Based on variations in biomass, cover and shoot density along the gradient, *S. herbacea* appears to 'prefer' a long-lasting snow cover (cf. Figs 1 and 4). Cover and biomass increased with longer snow duration, although variation in biomass was large, probably due to the small sample-size. In addition, there were local divergences from the main tendencies along the gradient which were also detectable in percentage cover (Fig. 4). The increase in shoot density down the gradient is more accentuated than the increase in biomass, and density keeps increasing even after maximum biomass and cover have been achieved. This implies a decrease in shoot-individual biomass which agrees with the tendency towards decreasing plant size with longer snow duration that was observed by Billings & Bliss (1959).

The growth of shoots decreased with longer snow duration and showed no decline towards the upper distribution limit (Fig. 4). The changes in shoot growth are probably valid for the growth of the plant as a whole, since there is no clear trend along the

gradient in the partitioning of biomass between above- and below-ground parts (Table 1). Thus maximum size and growth of individuals in the shoot population are found at the upper distributional limit of *S. herbacea* where the growing season is the longest.

The facts that maximum population density and maximum individual growth occur at separate locations suggest that the distribution of *S. herbacea* is restricted to late-exposed areas by competition from other plant species. The prostrate growth form of this species probably makes it an inferior competitor to most other vascular plants and possibly also to some of the moss species (Kershaw 1962). Increasing abundance of other species, mainly *Deschampsia flexuosa* and *Vaccinium myrtillus*, probably reduces the shoot density of *S. herbacea* towards its upper distributional limit by restricting the spread of rhizomes and the formation of shoots.

The lower average shoot age in the upper part of the transect may also be an effect of competition, reducing shoot survival (Fig. 6). However, additional shoot mortality could be caused by grazing. Insect grazing seems to have a more severe impact in this part of the transect (Fig. 3) and the periodic grazing of small rodents has been shown to be most intense in areas of intermediate snow cover (Emanuelsson 1984). A lower average shoot age would also have occurred in this section if it was colonized during the ten years prior to the study. However, this explanation seems unlikely since virtually no changes have been observed in the distribution of plant species during the six years of observations.

The differences in shoot growth showed a disproportionately wide range compared with the relatively slight differences in growing season. At 6.5 m, the accumulated shoot length was three times greater and weight five times greater than at 14.0 m. The difference in snow duration between these sites averaged only nine days or approximately 20% of the total length of the growing season and there were no appreciable differences in phenological rates (Fig. 3). However, the between-year variation in the amount of shoot increment seems to be of about the same order of magnitude as the variation in growing season length, i.e. $\pm 20\%$ (Wijk 1986).

Thus shoot growth within the gradient is probably affected by other environmental factors in addition to snow duration, e.g. nutrient availability, which changes with the amount and quality of litter (Miller 1982) and decomposition, which is probably inhibited in the lower part of the transect due to temporary waterlogging. However, the differences in shoot growth are most likely also associated with differences in the age of individuals and rhizomes within the transect. Competition and grazing probably select young and vigorous plants at the upper part of the transect, while the life-span of individuals as well as of shoots increases as the severity of the physical environment increases (cf. Callaghan & Collins 1981).

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REFERENCES

- Billings, W. D. & Bliss, L. C. (1959). An alpine snowbank environment and its effect on vegetation, plant development and productivity. *Ecology*, **40**, 388–397.
- Callaghan, T. V. & Collins, N. J. (1981). Life cycles, population dynamics and the growth of tundra plants. *Tundra Ecosystems: A Comparative Analysis*. IBP 25. (Ed. by L. C. Bliss, J. B. Cragg, D. W. Heal & J. J. Moore) pp. 257–284. Cambridge University Press.
- Emanuelsson, U. (1984). *Ecological effects of grazing and trampling on mountain vegetation in northern Sweden*. PhD. thesis, University of Lund.
- Flock, J. W. (1978). Lichen bryophyte distribution along a snow-cover soil-moisture gradient, Niwot Ridge, Colorado. *Arctic and Alpine Research*, **10**, 31–47.
- Gjaerevoll, O. (1956). The plant communities of the Scandinavian alpine snow-beds. *Det Kunglige Norske videnskabers selskabs skrifter*, **1**, 1–405. Trondheim.
- Gjaerevoll, O. & Bringer, K.-G. (1965). Plant cover of the alpine regions. *Acta Phytogeographica Suecica*, **50**, 257–268.
- Kershaw, K. A. (1962). Quantitative ecological studies from Landmannahellir. I. *Eriophorum angustifolium*. *Journal of Ecology*, **50**, 163–169.
- Knight, D. H., Rogers, B. R. & Kyte, C. R. (1977). Understorey plant growth in relation to snow duration in Wyoming subalpine forest. *Bulletin of the Torrey Botanical Club*, **104**, 314–319.
- Lid, J. (1979). *Norsk og Svensk Flora*. Det Norske Samlaget. Oslo.
- Lindholm, F. (1955). Sunshine and cloudiness in Sweden 1901–1930. *Geografiska annaler*, **37**, 1–50.
- Miller, P. C. (1982). Environmental and vegetational variation across a snow accumulation area in montane tundra in central Alaska. *Holarctic Ecology*, **5**, 85–98.
- Palmer, W. H. & Miller, A. K. (1961). Botanical evidence for the recession of a glacier. *Oikos*, **12**, 75–86.
- Resvoll, T. R. (1917). Om planter som passer til kort og kald sommer. *Arkiv for matematik og naturvidenskab*, **35**, 1–224. Kristiania.
- SHMI (1979). *Månadsöversikt över väderlek och vattentillgång*. Yearbook, **61**. Sveriges meteorologiska och hydrologiska institut. Stockholm.
- Sokal, R. R. & Rohlf, F. J. (1969). *Biometry*. Freeman. San Francisco.
- Sørensen, T. (1941). Temperature relations and phenology of the north-east Greenland flowering plants. *Meddelelser om Grönland*, **125**, 1–305.
- Wallén, C. C. (1948). Glacial-meteorological investigations on the Kårsa glacier in Swedish Lapland 1942–1948. *Geografiska annaler*, **30**, 451–672.
- Wijk, S. (1986) in press. Influence of climate and age on annual shoot increment in *Salix herbacea*. - *Journal of Ecology* 74.

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INFLUENCE OF CLIMATE AND AGE ON ANNUAL SHOOT INCREMENT IN *SALIX HERBACEA*

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SUMMARY

(1) Shoots of the dwarf shrub *Salix herbacea* were collected from three alpine snow-bed sites in northern Sweden. Multiple regression analysis was used to examine the importance of shoot age, mean monthly temperature and precipitation in determining annual shoot increment.

(2) Shoot age accounted for 39–48% of the within-shoot variation in length of the annual stem segments, which showed a logarithmic decline throughout the life-span of the shoot.

(3) Climatic variables contributed little to the total variation in annual increment. However, temperatures during the intense snow-melt period (May and June) during the year before growth, accounted for about 80% of the between-year variation in two of the three samples. This suggests that growing season length limits the carbohydrate stores available for the following year's shoot increment.

INTRODUCTION

Shoot growth in woody plants is affected by environmental factors, as well as factors inherent to the plant such as age and apical dominance. Much has been written on factors influencing shoot growth in trees; however, few studies have been conducted on dwarf shrubs. The annual shoot increment in the rhizomatous dwarf shrub *Salix herbacea** has previously been shown to decrease along gradients of increasing snow cover (Wijk 1986). The aim of this study was to elucidate how the annual shoot increment in *S. herbacea* is affected by shoot age and climatic variation. *Salix herbacea* is a suitable species for such a study since its markedly segmented stem facilitates shoot-age determinations and allows for retrospective studies of climatic influences.

All plants age and will eventually experience a decrease in growth rate. However, rhizomatous plants reproduce vegetatively. Thus, ageing acts not on the individual as a whole but on the separate parts of the plant which inevitably become senescent and display decreased growth rates. Flower-Ellis (1971) observed decreases in average lengths of successive annual shoot generations in the dwarf shrub *Vaccinium myrtillus* and this seems to be general for woody plant modules (White 1980). Therefore, a similar age-dependent pattern could be expected in *S. herbacea* annual shoot increments.

It seemed reasonable to hypothesize that any between-year variations in annual shoot increments unrelated to shoot age were mainly due to climatic variations. In trees, ambient conditions during bud development affect the following year's shoot elongation (Kozlowski 1964; Clements 1970). This is probably due to morphological constraints on the current shoots already present within the bud, implying that shoot extension does not involve growth of new organs (Larsson 1979). In addition, arctic and alpine *Salix* species, as well

* Nomenclature for vascular plants follows Lid (1979).

as other woody plants, evidently use stored resources for rapid shoot elongation early in the season (Bliss 1956, 1966; Billings & Bliss 1959; Mooney & Billings 1960; Berg, Kjelvik & Wielgolaski 1975). Thus, the amount of shoot elongation is, in most cases, more affected by the climate of the previous growing season than by conditions of the current year (Kozłowski 1964; Larsson 1979). Data on previous year's climate were therefore also included in the regression analyses of shoot growth in this study.

MATERIALS AND METHODS

Study site

Field work was carried out in an alpine area (600 m altitude), close to Vassijaure, Sweden (68°25'N, 18°15'E), 15 km west of Lake Torneträsk in the northern part of the Scandinavian mountain range. The topography of the area is characterized by glacio-fluvial terraces with snow accumulating on the leeward slopes. The zonation of vegetation along topographical gradients with varying snow cover has been mapped in eleven transects (S. Wijk, unpublished data). The plant material analysed in the present study was sampled from two of these transects, T I and T II. Both had easterly aspects and declinations of approximately 25°. The vegetation of the sample sites belongs to the alliance '*Deschampsio-Anthoxanthion*' according to the classification by Gjaerevoll (1950), and is characteristic for early snow-free, seasonally-wet snow-beds on acid soils. Besides *S. herbacea*; *Deschampsia flexuosa*, *Carex bigelowii*, *C. brunnescens* and *Anthoxanthum odoratum* were abundant vascular species at the sample sites.

The climate of the area is maritime with prevailing westerly winds. Annual precipitation averages 807 mm and the mean annual temperature is -1.4 °C (SMHI 1979). Climatic records since 1970 have been available for a meteorological station situated at Katterjåkk, 5 km west of the research area. Prior to 1970, the previous station was located at Riksgränsen, 2 km west of the present one. At the study site, temperature and humidity were recorded with a thermohygrograph while precipitation was measured at irregular intervals during the summer months. During 1979-82, the extent to which snow covered the transects was measured weekly from late May until melting was completed. The dates at which the snow had melted at the sample sites are presented in Table 1.

Shoot sampling

A *Salix herbacea* plant generally consists of a large number of aerial shoots interconnected by an extensive rhizome system. Shoots can be distinguished from rhizomes since the former have segmented stems. Each segment corresponds to the annual shoot increment (Resvoll 1917; Wijk 1986).

Plant material was sampled at T I-9.0 m (1977), T II-6.0 m (1979) and T II-11.0 m

TABLE 1. Mean temperatures during May and June and snow release dates at the sample sites used in studies of *Salix herbacea* during 1979-82. For details see text.

Year	Snow release (date)			Mean temperature (°C)	
	T I-9.0	T II-6.0	T II-11.0	May	June
1979	June 24	June 22	June 26	1.0	7.7
1980	June 19	June 17	June 21	2.3	10.5
1981	July 6	July 3	July 10	2.3	4.5
1982	July 12	July 11	July 19	1.0	3.3

(1978). Transect positions refer to distances (in metres) to the top of the topographical gradient. All samples were collected during mid-August and were subsequently stored at -15°C . Three transects, 0.8 m long and perpendicular to the gradient of snow cover, were delineated (Wijk 1986). Shoots on the transects were cut at their rhizome junctions. The length of each stem segment was measured (± 0.2 mm) and the branching pattern of each shoot was recorded.

Treatment of the data

Logarithms of the segment lengths were normally distributed and were used for the subsequent calculations. To reduce some of the considerable size variation between individual shoots, segment lengths were standardized by subtracting the average length increment of the shoot during its first six years of growth from its observed length. Shoots younger than six years and segments produced before 1968 were excluded. The final material comprised a total of 533 annual stem segments from 39 shoots produced between 1968 and 1979 (Table 2).

Since the shoots were continuously ageing during the observation period, the effects of shoot age and climate on growth could not be entirely separated. Therefore the data were analysed by means of a multiple regression technique, using step-wise inclusion. The logarithm of relative segment length was used as the dependent variable. If more than one segment had been produced by a shoot in one year, i.e. branching had taken place, the mean value was used. Independent variables included shoot age at the time of segment production and monthly mean temperature and precipitation from May to September for both the year of segment growth and the previous year (data from Riksgränsen and Katterjåkk).

Coefficients of shoot age were inserted into the multiple regression equations with the one or two most important climatic variables. Residual variation between years was analysed by means of a one-way analysis of variance. It was then possible to calculate the amount of variation between years accounted for by the climatic variables in the regression.

TABLE 2. Number of shoots and segments analysed, branching frequency and mean shoot-increment of *Salix herbacea* at sample sites on transects TI and TII.

	Sample			Total
	TI-9.0	TII-6.0	TII-11.0	
No. of shoots ≥ 6 years old	11	11	17	39
No. of annual stem segments	111	188	234	533
<i>n</i> for regressions and analyses of variance	86	103	159	348
Mean segment no. shoot ⁻¹ year ⁻¹ between ages 1-6 years	1.2	1.5	1.2	
Mean increment (mm) shoot ⁻¹ year ⁻¹ between age 1-6 years (backtransformation of log ₁₀ means)	3.1	6.0	3.9	

RESULTS

Age-dependent growth

The regression analyses for each of the three samples showed a highly significant, negative relationship between shoot increment and shoot age (Table 3). An increase of five years in age corresponded to a reduction in shoot increment by about 50% (Fig. 1). Shoot

TABLE 3. Multiple regression of $\log_{10}$ relative shoot increment of *Salix herbacea* at sample sites on transects TI and TII with step-wise inclusion of significant ($P \leq 0.05$) variables—shoot age (years), T (temperature during year of growth ($^{\circ}\text{C}$)), and TB (temperature during year before growth ($^{\circ}\text{C}$)). Symbols: **, $P \leq 0.01$; ***, $P \leq 0.001$.

Sample	Step	Variable	Regression coefficient	Increase in r^2
T I-9.0	1	Shoot age	-0.055***	0.39
	2	T August	-0.076***	0.07
	3	TB May	-0.085**	0.06
		Constant	0.97	Total: 0.52
T II-6.0	1	Shoot age	-0.055***	0.48
	2	TB May	0.044**	0.04
		Constant	0.15	Total: 0.52
T II-11.0	1	Shoot age	-0.045***	0.39
	2	TB June	0.031***	0.05
		Constant	-0.078	Total: 0.44

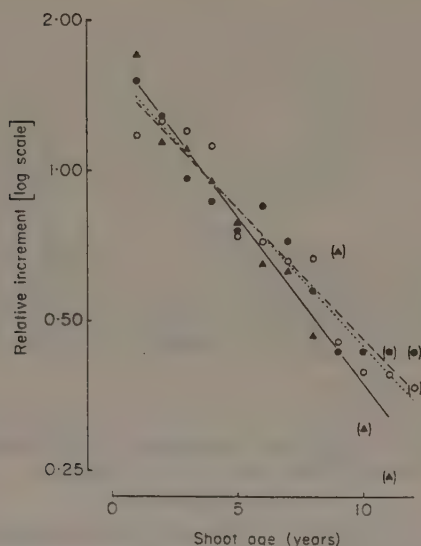


FIG. 1. Age-dependent growth of *Salix herbacea*. The average relative shoot lengths within each age class are plotted on a logarithmic scale where a value of 1.00 corresponds to the mean annual length increment for shoots aged 1–6 years. Linear regressions on individual values are for : T I-9.0 ($\blacktriangle$, —); T II-6.0 ($\bullet$, ---); T II-11.0 ($\circ$,). Points are shown in parentheses when $n < 5$.

age was always entered at step one of the multiple regressions and explained 39–48% of the variation in segment length. In all samples, more than 90% of the variation between age classes was accounted for by simple linear regression.

Growth in relation to climatic variation

Climatic data recorded at the study area were strongly correlated with similar data from the meteorological station at Katterjåkk. Mean temperatures calculated for the months

May to September (1978–80), showed a correlation coefficient of $r = 0.99$. Precipitation measured during eight observation periods, each of 22–43 days, between June and September (1979–81) at the study site showed a correlation of $r = 0.97$ with analogous data from the meteorological station.

The climatic variables were of much less importance than shoot age when considering total variation in segment length (Table 3). In sample T II–6.0, the May temperature in the year before growth (TB May) showed a significant positive relationship to segment length, while the second most important climatic variable, TB June, was not significant ($P < 0.1$). However, TB June was the only significant climatic variable in sample T II–11.0 and had a positive regression coefficient. In contrast, regression analysis of data from sample T I–9.0 showed negative relationships between shoot growth and the two most important climatic variables, T August (August temperature in the year of growth) and TB May.

The results presented so far have referred to the significance of the variance due to regression over the pooled residual variance. In addition, analyses of variance were carried out to determine how much of the between-year variation could be accounted for by climatic variables in the regressions (Table 4). After shoot age was accounted for, the residual between-year variation was reduced by 55% in sample T II–6.0 by addition of TB May and by 79% when TB June was also entered. Although the variance between years was not significant, the regression with these variables was highly significant. In sample T II–11.0, one variable, TB June, accounted for 82% of the residual variation between years. The most important climatic variable in sample T I–9.0, T August, accounted for 50% of the between-year variation. A graphical presentation of the annual mean of residuals for direct comparison with the most important temperature variables is shown in Fig. 2. The between-year variation in shoot increment was of about the same order of magnitude as the variation in growing season length, i.e. approximately $\pm 20\%$ if growth is assumed to cease in early September (Table 1).

TABLE 4. Analysis of residual between-years variance in studies of shoot increment of *Salix herbacea* at sites along transects TI and TII. Regressions on residuals were calculated with the following independent variables: T I–9.0, mean August temperature; T II–6.0, mean temperatures during May and June the year before growth; and T II–11.0, mean June temperature the year before growth. Residuals were achieved by inserting the coefficient of shoot age into the regressions.

Symbols: *, $P \leq 0.05$; ***, $P \leq 0.01$.

Source of variation	Sample					
	T I–9.0		T II–6.0		T II–11.0	
	d.f.	F	d.f.	F	d.f.	F
Between years	9	2.5*	11	1.1	10	2.2*
linear regression	1	8.1*	2	17.8***	1	40.8***
deviations from linear regression	8	1.4	9	1.0	9	1.0
Within-years	76		91		148	

DISCUSSION

Age-dependent growth

The relative length of *S. herbacea* annual stem segments decreases with increasing shoot age. Unlike the productivity decrease due to senescence in mature plants, the annual shoot increment has already begun to decrease during the first years of growth. According to

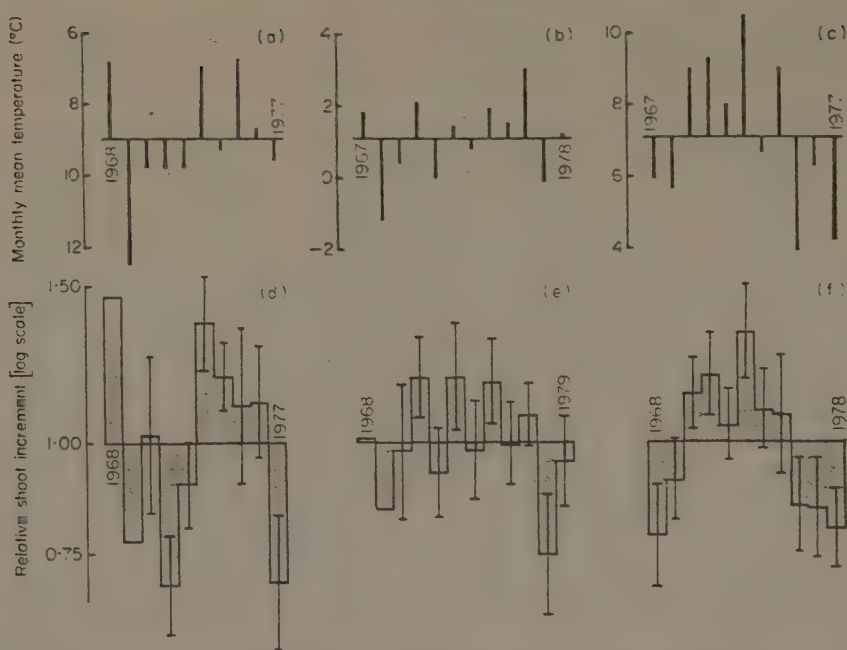


FIG. 2. Influence of climate on annual shoot increment of *Salix herbacea*. The most important climatic variable from each sample is shown together with the relative shoot increment for direct comparison of individual years. Temperature bars are drawn from a baseline representing the average monthly mean over the observation period. Analogous annual deviations from the average shoot increment in each sample are presented by bars (with standard errors if $n \geq 5$). (a) Mean August temperature (note reversed scale due to the negative relationship); (b) mean May temperature; (c) mean June temperature; (d) relative growth in sample T I-9-0; (e) relative growth sample T II-6-0; (f) relative growth in sample T II-11-0.

White (1980), decreasing module size with age in woody plants is closely associated with an increase in module numbers. Log-linear relationships have previously been shown to occur between branch order and branch length in trees, implying a constant 'length ratio' between the branch lengths of successively lower orders (Leopold 1971). However, the present study shows a log-linear decrease in the size of successive generations of segments within a single shoot axis with few branches. Thus, the age-dependent decrease in shoot increment is probably not directly associated with branching.

Although the branching frequency was considerably higher at the site with the longest growing season (T II-6-0, Table 2), the relationship between age and annual increment was essentially the same for all sites (Table 3, Fig. 1). This suggests that excess energy resulting from a longer growing season is invested in new branch production: while the length ratio between successive segments remains constant, thus maintaining the dwarf-shrub growth form.

There are several possible mechanisms for the age-dependent decrease in shoot increment. Nutrient and water deficiencies may arise from restricted root growth (Borchert 1978) or from decreasing transport capacity (Zimmermann & Brown 1971) due to reductions in xylem and phloem formation with age. The respiratory burden and

translocation resistance increase as the shoot grows in size, thus requiring larger energy expenditures. Wallén (1983), suggested that the ageing of *Calluna vulgaris* stems resulted from increases in translocation path length. In addition, a reduction in apical dominance could promote translocation of assimilates and recycling of nutrients from older to younger shoots, as previously shown in rhizomatous plants (Callaghan 1977, 1980).

The small size of *Salix herbacea* shoots has allowed this species to exploit very different environments. Thus, it can survive in wind-exposed fell fields with a minimum of snow protection as well as under deep snow packs where mechanical pressures would damage larger shoots. However, the small size also reduces the ability of *S. herbacea* to compete against taller vascular plants, thus restricting its distribution and abundance in areas more favourable for plant growth (Wijk 1986).

Climate-dependent growth

Much of the between-year variation (i.e. not related to shoot age) could be accounted for by variation in a few simple climatic variables. In samples T II-6.0 and T II-11.0 there was a positive relationship between shoot increment and the previous year's May and June temperatures, respectively. Because no growth occurs before the snow cover has melted (mid-June at the very earliest) it is probably the influence of temperature on snow duration that affects the following year's shoot growth. The snow duration at T II-6.0 was somewhat shorter than at T II-11.0 and, as expected, May temperature was a better predictor of the following year's shoot growth than was June temperature. Precipitation probably does not affect the melting rate as much as temperature and did not significantly affect shoot growth in this study. Neither did the climate during the main growing season, July to early September, affect annual increment. The influence of current climate on growth is probably reduced, for the most part, by temperature acclimation (cf. Billings & Bliss 1959). Thus, the accumulation of assimilates necessary for shoot elongation during the following year is largely dependent on the length of the growing season.

There is no sensible explanation for the negative relationship found between shoot increment and monthly mean temperatures, i.e. T August and TB May, in sample T I-9.0. In addition, shoot extension has probably ceased by early August (cf. Bliss 1956); therefore the significance of T August is meaningless. Thus, the outcome of regression from this sample is probably of little biological significance but may be ascribed to non-causal correlations which commonly occur in multiple regression analyses.

Climatic variables contributed very little to the total amount of variation in annual shoot increment (Table 3). However, variation due to shoot age and other factors intrinsic to the plant does not affect the total productivity of a stable population. Thus, the climatic influence may be of considerably greater importance for the variation in *S. herbacea* productivity than the regression results indicate.

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REFERENCES

- Berg, A., Kjelvik, S. & Wielgolaski, F. E. (1975). Distribution of ^{14}C photosynthates in Norwegian alpine plants. *Fennoscandian tundra ecosystems, part 1: Plants and microorganisms*. (Ed. by F. E. Wielgolaski), pp. 208–215. Springer, Berlin.
- Billings, W. D. & Bliss, L. C. (1959). An alpine snowbank environment and its effect on vegetation, plant development and productivity. *Ecology*, **40**, 388–397.
- Bliss, L. C. (1956). A comparison of plant development in microenvironments of arctic and alpine tundras. *Ecological Monographs*, **26**, 303–337.
- Bliss, L. C. (1966). Plant productivity in alpine micro environments on Mt. Washington, New Hampshire. *Ecological Monographs*, **36**, 125–155.
- Borchert, R. (1978). Feedback control and age-related changes of shoot growth in seasonal and nonseasonal climates. *Tropical trees as Living Systems*. (Ed. by P. B. Tomlinson & M. H. Zimmermann), pp. 497–515. Proceedings of the Fourth Cabot Symposium. Cambridge University Press.
- Callaghan, T. V. (1977). Adaptive strategies in the life cycle of South Georgian graminoid species. *Adaptions within antarctic ecosystems*. (Ed. by G. A. Llano). Proceedings of the Third S.C.A.R. Symposium on Antarctic Biology, Smithsonian Institution. Washington.
- Callaghan, T. V. (1980). Age-related patterns of nutrient allocation in *Lycopodium annotinum* from Swedish Lapland. Strategies of growth and population dynamics of tundra plants 5. *Oikos*, **35**, 373–386.
- Clements, J. R. (1970). Shoot responses of young red pine to watering applied over two seasons. *Canadian Journal of Botany*, **48**, 75–80.
- Flower-Ellis, J. G. K. (1971). *Age structure and dynamics in stands of bilberry (Vaccinium myrtillus L.)*. Research notes 9. Department of Forest Ecology and Forest Soils, Royal College of Forestry. Stockholm.
- Gjaerøvoll, O. (1950). The snow-bed vegetation in the surroundings of Lake Tornetråsk, Swedish Lapland. *Svensk Botanisk Tidskrift*, **44**, 387–440.
- Kozłowski, T. T. (1964). Shoot growth in woody plants. *Botanical Review*, **30**, 335–392.
- Larsson, S. (1979). Climate as growth regulating factor in trees. I. A review of the literature. *Swedish Coniferous Forest Project, Technical Report 22*. Swedish University of Agricultural Science. Uppsala.
- Leopold, L. B. (1971). Trees and streams: the efficiency of branching patterns. *Journal of Theoretical Biology*, **31**, 339–354.
- Lid, J. (1979). *Norsk og Svensk Flora*. Second edition. Det Norske Samlaget. Oslo.
- Mooney, H. A. & Billings, W. D. (1960). The annual carbohydrate cycle of alpine plants as related to growth. *American Journal of Botany*, **47**, 594–598.
- Resvoll, T. R. (1917). Om planter som passer til kort og kold sommer. *Arkiv for matematik og naturvidenskab*, **35**, 1–224.
- SMHI (1979). *Månadsöversikt över Väderlek och Vattentillgång. Yearbook, Vol. 61*. Sveriges Meteorologiska och Hydrologiska Institut. Stockholm.
- Wallén, B. (1983). Translocation of ^{14}C in adventitiously rooting *Calluna vulgaris* on peat. *Oikos*, **40**, 241–248.
- White, J. (1980). Demographic factors in populations of plants. *Demography and Evolution in Plant Populations*. (Ed. by O. T. Solbrig), pp. 21–48. Botanical Monographs, Vol. 15. Blackwell Scientific Publications. Oxford.
- Wijk, S. (1986). Performance of *Salix herbacea* in an alpine snow-bed gradient. *Journal of Ecology*, **74**, 000–000.
- Zimmermann, M. H. & Brown, C. L. (1971). *Trees: Structure and Function*. Springer, New York.

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AGE STRUCTURE OF *SALIX HERBACEA* SHOOTS IN AN ALPINE SNOW-BED

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SUMMARY

(1) Aerial shoots of the dwarf shrub *Salix herbacea* were collected along an alpine snow-bed gradient. Shoot age was determined by counting the number of successive annual stem segments. Survivorship curves were derived from the age structure data.

(2) The major part of the shoot population showed a smooth age structure with a mean shoot age of 6.5 years and a half life of 9.0 years. Mortality was insignificant under 6 years of age, and showed a constant rate of 21% per year in older age classes. However, near the upper distribution limit of the species, where the snow cover is less, the mortality rate was higher, mean shoot age was 4.0 years and the half-life was 7.5 years. The differences in mortality are probably related to different intensities of competition and grazing and possibly also related to the conditions for layering.

(3) Variation in June temperature accounted for 50% of the variation in size of age classes 1 - 6 years. This suggests that early snowmelt promotes the recruitment of shoots. The July temperature of the previous year accounted for an additional 24 % of the variation in recruitment.

INTRODUCTION

Even though dwarf shrubs are major constituents of many vegetation types there is a scarcity of data concerning their demography and life history; partly because many dwarf shrubs show clonal growth. When the centre of an individual eventually dies, the growth of the genet can be maintained by distal rhizomes or by layering of the branches. Thus there can be great difficulties encountered when collecting and interpreting demographic data on whole plants (Harper 1980, Callaghan & Collins 1981, Callaghan & Emanuelsson 1985).

In contrast, aerial shoots generally exhibit a well defined life-span which is much shorter than that of the prostrate stems or rhizomes (Pelton 1953, Flower-Ellis 1971). Each shoot can be fairly independent with respect to carbohydrate economy (Wallén 1983) and may compete with other shoots for light, water, and nutrients. Thus the aerial shoots are plant subunits which, for many purposes, are more appropriate and certainly more accessible for studies of life history and ecology in dwarf shrubs than the more indefinite individuals or genets. (Harper & White 1974, Harper & Bell 1979).

Salix herbacea L. is a dwarf shrub widely distributed in alpine habitats of Europe. However, it is most abundant in unproductive environments associated with short growing seasons, and its competitive ability is probably inferior to that of most other vascular plants (Kershaw 1962, Wijk 1986a). The latter paper describes how the performance of this species varied along a snow duration gradient from the centre of a snowbed to its distribution limit. The present work examines the age structure and survival of shoots and the differences that occur within the gradient. It also includes an analysis of climatic influences on the yearly recruitment of shoots.

MATERIALS AND METHODS

The study site was an alpine snowbed, altitude 600 m, 2 km south-east of Vassijaure (68° 25' N, 18° 15' E) in northern Sweden. A transect, (18 m x 1 m) was laid out from the edge of a glaciofluvial terrace (referred to as level 0 m) down to the depression below. The transect represented a steep snow duration gradient, and in the section where *S. herbacea* occurred, i.e., below the 6.0 m level, the snow cover generally disappeared between mid-June and mid-July (Wijk 1986a).

TABLE 1. Shoot sampling specifications.

Sample year	Method	No. samples	No. shoots	Shoot age,	
				median	mean
1977	0.8 m transect	12	513	5	5.3
1978	1.0 dm ² quadrat	12	287	6	7.4
1980	6 x 0.38 dm ² cores	5	130	5	6.2
Total			930	5	6.1

The study is based on *S. herbacea* plant material that was sampled on three occasions (primarily for other purposes) along the transect in late summer. In 1977, aerial shoots were cut along twelve 0.8 m transects perpendicular to the main transect; in 1978, twelve 1 dm² samples were taken at 1.0 m intervals; and in 1980, six 0.38 dm² cylinder cores were taken at five levels in the transect (Table 1). Details of the sampling procedures were described in Wijk (1986a).

There is generally a clear morphological distinction between the aerial shoot and the rhizome, since the shoot stem is segmented by the bud-scale scars formed each year. Shoot age was determined by counting the number of successive annual stem segments. Population age structures were calculated after pooling shoot material from the different sampling occasions. The shoot population above the 8.0 m level in the transect was treated separately, since it differed from the population below. The log-normal curves for the same age structures were calculated for interpretation as survivorship curves.

The age-structure data for the shoot population below the 8.0 m level indicated no considerable mortality before the age of 6 years. Therefore it was assumed that the number of shoots in age classes 1 - 6 years corresponded to the recruitment of shoots in each of the 6 years preceding the year of sampling. Thus it was possible to estimate the variation in shoot recruitment during the period 1972 - 1980. The climatic influence on shoot recruitment was analyzed by a step-wise multiple regression with monthly mean temperatures of May - September the year of recruitment and the year before. The temperature data were obtained from the meteorological station at Katterjåkk, 5 km west of the study site.

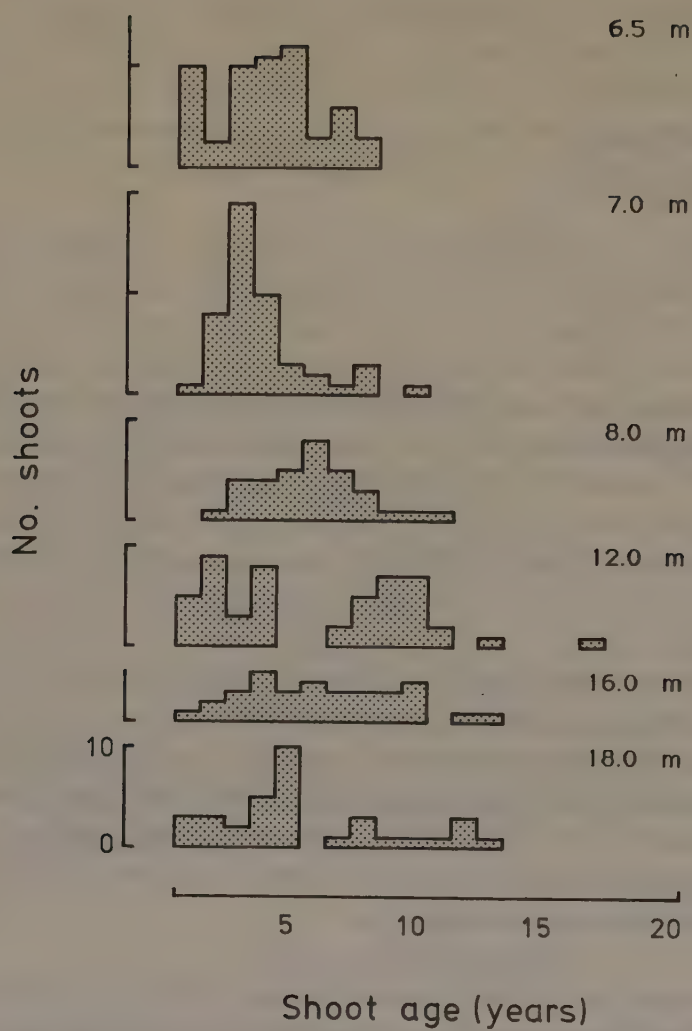


FIG. 1. Age structures in some individual samples from 1977.

RESULTS

The age class distribution of individual samples was very irregular, and there were often two or more peaks (Fig. 1). Mean shoot age varied between 5 to 8 years with few exceptions. At the upper part of the transect, mean shoot age was significantly lower due to the lack of old shoots (Fig. 2). The deviating high means in the middle of the transect were probably due to the small sample area used in 1978. Mean shoot age for the populations above and below 8.0 m were 4.0 and 6.5 years, respectively.

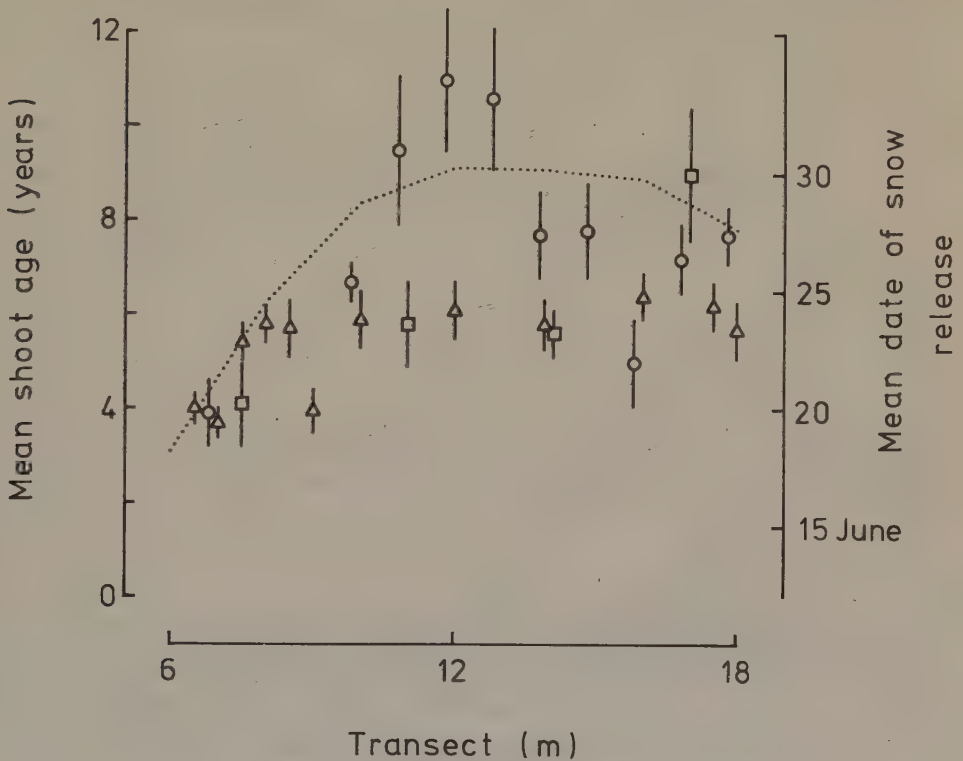


FIG. 2. Variation in mean shoot age ($\pm$ S.E.) along the transect; sampling year: 1977 (Δ), 1978 ($\circ$), and 1980 ($\square$) (samples with $n < 5$ are excluded). The dotted curve shows the average dates of snow release in 1978-1983.

The pooled age structures showed minor fluctuations and are probably representative estimates for the shoot populations above and below the 8.0 m level (Fig. 3). At levels ≥ 8.0 m the age classes 1 - 6 years were of the same order of size, while the older age classes gradually declined in size. The maximum shoot age recorded was 32 years. The same age structure plotted on a logarithmic scale resulted in a fairly smooth curve. When interpreted as a survivorship curve, it implied 100% shoot survival until the age of 6 years, while there was a fairly constant mortality rate of 21 % per year in older age classes ($r^2 = 0.90$). The shoot population above the 8.0 m level showed considerably higher mortality and there were no shoots older than 10 years. The half-lives of shoots (i.e., the age at which the population is reduced by 50%) above and below 8.0 m were 7.5 and 9.0 years, respectively.

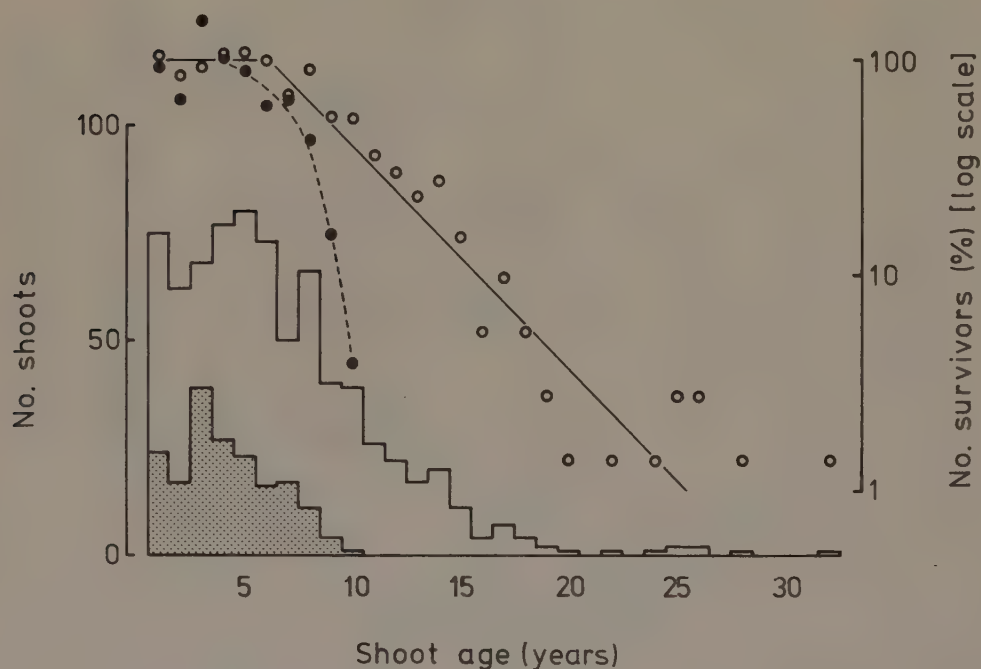


FIG. 3. Shoot age-class distributions and corresponding survivorship curves at transect levels < 8.0 m (shaded, $\bullet$; $n = 179$) and ≥ 8.0 m (unshaded, $\circ$; $n = 751$). Before log-transformation shoot numbers were expressed as percentages of the average size of age classes 1 - 5 years (< 8.0 m) and 1 - 6 years (≥ 8.0 m). Line from linear regression on age classes 6 - 32 years ($\log y = 2.66 - 0.105 x$; $r^2 = 0.90$); dashed curve fitted by hand.

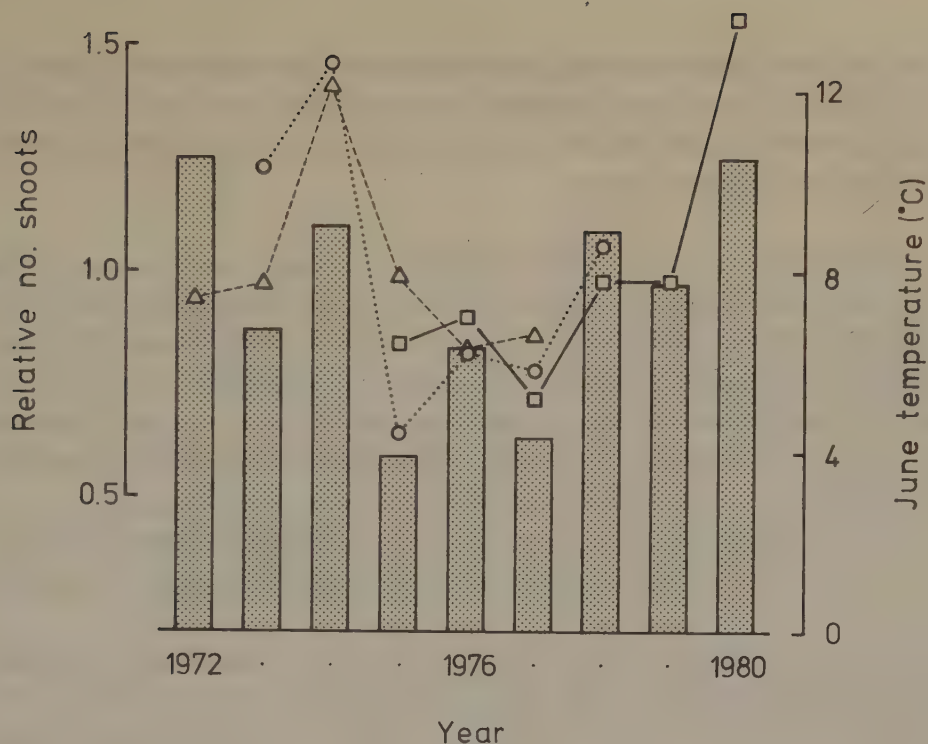


FIG. 4. Relative size of shoot age classes 1 - 6 years in relation to the June temperature (columns) in the year of recruitment. Samples from year 1977 (Δ), 1978 ($\circ$), and 1980 ($\square$).

Variation in shoot recruitment between years appeared to be strongly climate-dependent. June temperature alone accounted for 50 % of the variation in the relative size of age-classes 1 - 6 years (Fig. 4), and the multiple regression where July temperature the year before recruitment was also significant accounted for 74% of the variation ($P < 0.001$).

DISCUSSION

Derivation of survivorship curves from time-specific observations of population age structure are justified only if the age structure is stable with time (Deevey 1947). The shoot material used in this study was collected during a 4 year period and showed no trend in mean or median shoot age (Table 1, Fig. 2). Thus even if recruitment and mortality may vary somewhat between years, the population is likely to be relatively stable. The peaks in the age

class distribution of individual samples are not synchronised in time, and consequently they are not primarily associated with climatic fluctuations among years (Fig. 1). More likely, these peaks developed because most shoots in a sample emerged during a short period from a small number of prolific rhizomes.

The survivorship curve of *S. herbacea* shoots was intermediate between Deevey types I and II with an initial low mortality which increased and became constant after about 5 years of age (Fig. 3). Similar survival curves have been reported for other plants with perennial shoots or tillers, and the low mortality of young shoots is probably associated with the access to carbohydrates and other nutrients supplied by the main rhizome during the first years of growth (Flower-Ellis 1971, Forrest 1971, Fetcher & Shaver 1983, Callaghan & Emanuelsson 1985). When the shoot grows older it becomes more dependent on its own productivity and may also start to supply new shoots emerging from the rhizome. The ageing of shoots is also associated with a continuous decrease in incremental growth (Wijk 1986b).

The half-life of *S. herbacea* shoots (below 8.0 m) was 9 years, which is of the same order of magnitude as reported for other woody, rhizomatic plants (Pelton 1953, Flower-Ellis 1971). Since this is a very short life-span compared with the longevity of individual plants, shoot senescence is probably under internal genetic control. However, the shorter half-life above the 8.0 m level (7.5 years) might be due to external factors such as competition and grazing (Wijk 1986a). The differences in age-structure might also depend on conditions that affect the shoots' ability to increase their life-span by layering. The prostrate growth form and thin humus layer associated with deep snow cover favour formation of adventitious roots from the stem. The more erect and rapidly growing shoots at lower snow depths are probably better suited for competing with other plants, but their layering ability is probably reduced and further inhibited by a thicker humus layer. A very similar environmentally induced difference in survival curves has been described for tillers of *Eriophorum vaginatum* growing in undisturbed and disturbed tundra sites (Fetcher & Shaver 1983).

The current year's June temperature and the previous year's July temperature accounted for as much as 74 % of the variation in shoot numbers among the age classes 1 - 6 years. This implies that the underlying assumption of 100 % shoot survival until the age of 6 years seems very appropriate. The June temperature affects the rate of snowmelt; therefore, the primary factor causing variation in shoot recruitment is probably growing season length. Wijk (1986a) showed that the previous year's May and June temperatures are the most important climatic variables responsible for the between-year variation in shoot incremental growth.

Thus a longer growing season appears to promote growth and shoot formation, and most likely it is increased mortality which reduces shoot density and limits the distribution of *S. herbacea* in the section of the gradient with the shortest period of snow cover.

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REFERENCES

- Callaghan, T.V. and Collins, N.J. (1981). Life cycles, population dynamics and the growth of tundra plants. - In: Bliss, L.C., Cragg, J.B., Heal, D.W. and Moore, J.J. (eds.). Tundra ecosystems: A comparative analysis. IBP 25. pp 257 - 284. Cambridge University Press.
- Callaghan, T.V. and Emanuelsson, U. (1985). - In: White, J. (ed.). The Population Structure of Vegetation. pp. 399 - 439. Junk Publishers, Dordrecht.
- Deevey, E.S. (1947). Life tables for natural populations of animals. - The Quarterly Review of Biology 22: 283 - 314.
- Fetcher, N. & Shaver, G.R. (1983). Life histories of tillers of *Eriophorum vaginatum* in relation to tundra disturbance. - Journal of Ecology 71:131 - 147.
- Flower-Ellis, J.G.K. (1971). Age structure and dynamics in stands of bilberry (*Vaccinium myrtillus* L.). - Research notes 9. Dept. forest ecol. and forest soils, Royal College of Forestry. Stockholm.
- Forrest, G.I. (1971). Structure and production of North Pennine blanket bog vegetation. - Journal of Ecology 59: 453 - 479.
- Harper, J.L. (1980). Plant demography and ecological theory. - Oikos 35: 244-253.
- Harper, J.L. & Bell, A.D. (1979). The population dynamics of growth form in organisms with modular construction. - In: Andersson, R.M. et al.(eds.). Population dynamics, the 20th symposium of the British Ecological Society. pp. 29 - 52. Blackwell, Oxford.
- Harper, J.L. & White, J. (1974). The demography of plants. - Annual Review of Ecology and Systematics 5: 419 - 463.
- Kershaw, K.A. (1962). Quantitative ecological studies from Landmannahellir. I. *Eriophorum angustifolium*. - Journal of Ecology 50: 163-169.
- Pelton, J. (1953). Studies on the life history of *Symphoricarpus occidentalis* Hook. in Minnesota. - Ecological Monographs 23: 17 - 39.
- Wallén, B. (1983). Translocation of ^{14}C in adventitiously rooting *Calluna vulgaris* on peat. - Oikos 40: 241-248.
- Wijk, S. (1986a) in press. Performance of *Salix herbacea* in an alpine snow-bed gradient. - Journal of Ecology 74.
- Wijk, S. (1986b) in press. Influence of climate and age on annual shoot increment in *Salix herbacea*. - Journal of Ecology 74.

